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A MANUAL OF HELMINTHOLOGY

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MEDICAL AND VETERINARY

WITHDRAWN

BY

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PREFACE

THERE is no need, at the present time, to emphasize the importance of helminthology in medical and veterinary science. The study of parasitic worms is generally regarded as a necessary part of the training of the veterinarian, and of that of the medical man who intends to practise in tropical or subtropical countries. The present outline of the subject is an attempt to bring together, under one cover, some account of the numerous species of worms parasitic in man and the domestic animals. The available descriptions of many of these species are only to be found scattered through a vast mass of periodical literature, much of which is not readily accessible. It is hoped, therefore, that this attempt to collect them may prove of some value to the practitioner as well as to the student, and may perhaps also be of some service, as a book of reference, to the increasingly large number of students of zoology who are specializing in helminthology.

As regards the illustrations, though in a few instances original drawings have been made from specimens in the British Museum (Natural History), the majority have been redrawn from existing figures by Miss F. R. Mold and Miss L. A. Sambon. The drawings copied by Miss Mold are distinguished by her initials. I wish to express to these ladies my grateful appreciation of their careful and painstaking work. To Miss Sambon and to my wife thanks are due for much help in other directions, especially in the preparation of the indices. It is also a pleasant duty to offer my best thanks to all the authors and publishers who have kindly allowed me to make use of their illustrations. Among these special mention must be made of Professor Warrington Yorke and Dr. P. A. Maplestone, from whose invaluable book on "The Nematode Parasites of Vertebrates" so many figures have been borrowed.

H. A. B.

SOUTH KENSINGTON,
December, 1928.

CONTENTS

INTRODUCTION - - - - -	PAGE ix
------------------------	------------

PART I

FLATWORMS - - - - -	1
i. THE FLUKES OR TREMATODES (<i>Class</i> TREMATODA) - - -	5
<i>Family</i> LEPODERMATIDÆ - - - - -	11
<i>Family</i> DICROCÆLIDÆ - - - - -	14
<i>Family</i> OPISTHORCHIDÆ - - - - -	18
<i>Family</i> HETEROPHYIDÆ - - - - -	22
<i>Family</i> TROGLOTREMATIDÆ - - - - -	27
<i>Family</i> PHILOPHALTHALMIDÆ - - - - -	29
<i>Family</i> FASCIOLIDÆ - - - - -	30
<i>Family</i> BUNODERIDÆ - - - - -	34
<i>Family</i> CYCLOCÆLIDÆ - - - - -	34
<i>Family</i> NOTOCOTYLIDÆ - - - - -	36
<i>Family</i> ECHINOSTOMATIDÆ - - - - -	38
<i>Family</i> PSILOSTOMIDÆ - - - - -	44
<i>Family</i> HARMOSTOMIDÆ - - - - -	45
<i>Family</i> SCHISTOSOMATIDÆ - - - - -	46
<i>Family</i> STRIGEIDÆ - - - - -	52
<i>Family</i> PARAMPHISTOMIDÆ - - - - -	55
ii. THE TAPEWORMS OR CESTODES (<i>Class</i> CESTOIDEA) - - -	62
(a) <i>Order</i> BOTHRIOCEPHALIDEA - - - - -	66
<i>Family</i> DIPHYLLOBOTHRIDÆ - - - - -	66
(b) <i>Order</i> TÆNIIDEA - - - - -	75
<i>Family</i> MESOCESTOIDIDÆ - - - - -	77
<i>Family</i> ANOPLOCEPHALIDÆ - - - - -	79
<i>Family</i> DAVAINIIDÆ - - - - -	90
<i>Family</i> DILEPIDIDÆ - - - - -	96
<i>Family</i> HYMENOLEPIDIDÆ - - - - -	102
<i>Family</i> TÆNIIDÆ - - - - -	110

PART II

	PAGE
ROUNDWORMS - - - - -	119
i. THE THREADWORMS OR NEMATODES (<i>Class</i> NEMATODA) - - -	121
(a) <i>Order</i> ASCARIOIDEA - - - - -	128
<i>Family</i> ASCARIDÆ - - - - -	128
<i>Family</i> HETERAKIDÆ - - - - -	135
<i>Family</i> KATHLANIIDÆ - - - - -	139
<i>Family</i> OXYURIDÆ - - - - -	140
<i>Family</i> RHABDITIDÆ - - - - -	143
(b) <i>Order</i> STRONGYLOIDEA - - - - -	146
<i>Family</i> STRONGYLIDÆ - - - - -	147
<i>Family</i> ANCYLOSTOMIDÆ - - - - -	163
<i>Family</i> METASTRONGYLIDÆ - - - - -	171
<i>Family</i> TRICHOSTRONGYLIDÆ - - - - -	178
<i>Family</i> AMIDOSTOMIDÆ - - - - -	199
(c) <i>Order</i> FILARIOIDEA - - - - -	202
<i>Family</i> FILARIIDÆ - - - - -	203
<i>Family</i> PHILOMETRIDÆ - - - - -	221
<i>Family</i> SPIRURIDÆ - - - - -	223
<i>Family</i> GNATHOSTOMIDÆ - - - - -	249
(d) <i>Order</i> DIOCTOPHYMOIDEA - - - - -	252
<i>Family</i> DIOCTOPHYMIDÆ - - - - -	252
(e) <i>Order</i> TRICHINELLOIDEA - - - - -	255
<i>Family</i> TRICHINELLIDÆ - - - - -	255
ii. THE ACANTHOCEPHALA OR THORNY-HEADED WORMS - - -	266
<i>Family</i> ECHINORHYNCHIDÆ - - - - -	269
<i>Family</i> GIGANTORHYNCHIDÆ - - - - -	271
INDEX TO PARASITES OF MAN AND PRINCIPAL DOMESTIC ANIMALS, ARRANGED UNDER THEIR HOSTS - - - - -	277
GENERAL INDEX - - - - -	285

INTRODUCTION

HELMINTHOLOGY is a branch of zoology in which there has, during the last few decades, been a very considerable revival of interest. The economic importance of parasites of all kinds has been more widely recognized, and it is this fact, doubtless, which has led a very large number of biologists in all parts of the world to devote themselves to their study. In no field is this renewed activity more apparent than in that of the parasitic worms. As a result, there has grown up an immense modern literature, to which a larger number of contributions is being added every year. The subject of helminthology has therefore become a very large one, and that portion of it which immediately concerns man and the commoner domestic animals is but a relatively small part of the whole field.

To deal exhaustively with even this small part of the subject, a work of encyclopædic dimensions would be required. The present book makes no claim to do this. On the contrary, one of its principal aims is to be as brief and concise as possible. The primary object which the writer has had in view is to provide such short descriptions of the genera and species as it is hoped, with the aid of the illustrations, may be found helpful to the reader in obtaining at least an approximate determination of most of the parasites with which he is likely to meet.*

All matter of secondary importance from this point of view will be treated with the utmost brevity, or excluded altogether. Full and detailed descriptions and full synonymies of all the species dealt with are out of the question, and the information given about each genus and species will generally be confined to a brief description of its occurrence and morphology, together with the more important facts of its life-history, so far as they are known. With the clinical aspect of helminthology it is not intended to deal, though some slight references to the pathological effects of those parasites which are definitely injurious are often inseparable from the biological aspect, and will then be briefly made.

* It is to be hoped that no one will take the descriptions here given as a model for the description of new species, or regard them as embodying all the information which should be given in such a case.

In certain genera the species are so numerous and so much alike that the only suitable method of dealing with them seems to be to tabulate their more important distinctive characters. Tables will usually be employed for this purpose in preference to "keys," since the latter must often be highly artificial, are extremely liable to break down, and may prove very misleading.

The general plan of the work is to follow as "natural" a classification of the worms as our present knowledge of them makes possible. That is, the species will be dealt with in the order, as nearly as possible, of their own relationships to each other, without regard to the hosts in which they occur. An alternative plan might have been to deal with the parasites of each host-animal separately, but this would have involved a great deal of unnecessary repetition. A classified index to the parasites of the more important animals, or groups of animals, arranged under their hosts, will, however, be found at the end of the book.

It is somewhat difficult to draw the line at which an animal ceases to be "wild" and becomes "domestic." The scope of this book would be increased beyond reasonable bounds were it to include an account of the parasites of the elephant and various other animals which, in their respective countries, are practically domesticated. It has seemed advisable, therefore, to confine it, for the most part, to those of the animals which are universally domesticated in almost all parts of the world. Somewhat arbitrarily, perhaps, the Indian humped ox or zebu (*Bos indicus*), the domesticated "water-buffalo" (*Bos bubalus*), and the Asiatic and Arabian camels are included, and some reference is made to certain birds which are not strictly or exclusively farmyard poultry, though no attempt has been made to deal thoroughly with their parasites. On the other hand, the rabbit (though perhaps entitled to some consideration as being more than a children's pet) is only incidentally mentioned, along with various other creatures which are not of definite economic importance except as subjects of laboratory experiment.

It should be borne in mind that, for every species parasitic in man or in a domestic animal, there are probably many hundreds of species which occur chiefly or solely in wild animals, and that a sound system of classification, zoologically speaking, must envisage the whole. With this consideration in view, though it would be out of place in a work of this size to go into the matter of classification in great detail, a slight sketch of the present systematic arrangement of each group will be given at the beginning of the section dealing with it.

A word is, perhaps, necessary on the subject of nomenclature. The names here used for the parasites will be those which are believed to be most in accordance with a reasonable interpretation of the rules of the International Commission on Zoological Nomenclature. These names will usually be printed in heavy type. At the same time, for the convenience of those who may be more familiar with other names which have enjoyed long, though incorrect, use, the more common and well-known synonyms will generally also be given.



PART I
FLATWORMS

FLATWORMS

THE Flatworms (Platyhelminthes or Platyodes) are soft-bodied multicellular organisms, usually more or less flattened in what is regarded as the dorso-ventral direction. In general form they are bilaterally symmetrical, and anterior and posterior ends can be distinguished, though in some groups (*e.g.*, the Cestodes) it is doubtful which end should properly be considered anterior. When the openings of the genital ducts are not (as they are in many Cestodes) lateral in position, that surface on which they are situated is usually called the ventral surface. In some of the free-living groups of flatworms the body is covered with a cellular epithelium bearing cilia. In the parasitic groups, however, this ciliated epithelium is absent (or is only present in the early larval stages), and the external covering of the body is a "cuticle" which may be smooth or may bear spines or "scales" of various kinds. Eyes, or patches of pigment known as "eye-spots" or ocelli, are frequently present in those forms which are free-living or ectoparasitic in habit, and occur occasionally in the early (free-swimming) stages of endoparasitic forms, but are absent in the adult forms which are truly endoparasitic.

In all flatworms a body-cavity (in the sense of a *cœlom*) is absent, or, more correctly speaking, the *cœlom* is reduced to the cavities of the gonads and excretory system, the various internal organs being embedded in, and supported by, a more or less spongy connective tissue known as parenchyme. The body may thus, for practical purposes, be regarded as solid. A *cœlom* being absent, there is no true segmentation. In the majority of the Cestodes, however, there is an apparent segmentation which is not comparable with that of Annelids, Arthropods, or higher animals.

The parasitic flatworms are usually provided with special clinging organs, in the form of disc-like muscular suckers, and frequently also with hooks or spines of various kinds. These organs enable the animals to attach themselves either to the external or to the internal surfaces of their hosts, and to avoid being swept away either by currents of water or by the peristaltic action of the host's viscera. Beneath the external cuticle of the body variously arranged layers of muscle-fibres are present. Generally speaking, there are longitudinal fibres which, by their con-

traction, cause the body to be shortened antero-posteriorly; transverse or circular fibres which tend to elongate it; and frequently oblique fibres capable of producing lateral movement of various kinds. These muscles are mainly superficial, lying in the outer, or as it is sometimes called, cortical, portion of the parenchyme.

An alimentary canal is not always present. When present, it is usually without a posterior opening. The mouth, when present, is usually ventral. In the Trematodes it is generally at or near the extreme anterior end, but in the free-living Turbellaria it is more often towards the middle of the body. The alimentary canal, when present, may be sac-like or variously branched. The nervous system of flatworms consists essentially of a bilaterally symmetrical system of nerve-fibres, connected anteriorly with a central mass or "brain" consisting of ganglia and transverse commissures. There are no blood-vessels, and no cavity which can be regarded as a hæmocœle. The excretory system consists of a more or less complex network of branching capillary tubes, ending in "flame-cells" (small terminal expansions each containing one or more bundles of vibratile cilia). The capillary vessels lead ultimately into larger vessels, and these sometimes into a "bladder." In the latter case there is usually a single external excretory pore, but in other cases the excretory system may have two or many openings.

The flatworms are, with very few exceptions, hermaphrodite animals—each individual being provided with both male and female reproductive organs. The reproductive system, in the parasitic forms with which we are particularly concerned, is usually complex. It is highly developed in consequence of the necessity for producing large numbers of offspring, in order that a sufficient number may survive the process of finding new hosts. Accordingly, the genital organs, with their immense variety of arrangement, have come to be of extreme importance in classification.

The male organs consist, essentially, of a testis, or two or more testes, with ducts (*vasa efferentia* and *vas deferens*) leading to an external pore. There is very commonly, though not always, an intromittent organ, or *cirrus*, through which the *vas deferens* opens, and this is generally contained in a more or less muscular pouch, the *cirrus-sac*. Connected with the *vas deferens*, or forming a mere local swelling in its course, there is frequently a reservoir for spermatozoa known as the *vesicula seminalis*. The essential parts of the female apparatus are the ovary (which is almost invariably single, though it may be more or less distinctly divided into two portions, or may be much subdivided into lobes); and a vagina, which sometimes functions only as a receptacle for spermatozoa, but sometimes also as a duct for the expulsion of fully-formed eggs. In connection with the vagina there may be a permanently or temporarily expanded reservoir

for spermatozoa, the *receptaculum seminis*. As a general rule, some kind of uterus is present. This is usually either a sac-like or a tubular reservoir for the eggs in their early stages of development after fertilization. There are also, in practically all flatworms, certain accessory glands concerned in the formation of the eggs. These are the yolk-glands, or vitelline glands, which commonly consist of numerous groups of follicles, and discharge their products (yolk-cells) through ducts ultimately joining the oviduct, by which eggs pass from the ovary to the uterus; and the "shell-gland," which is also connected with the oviduct.

The larval development of the flatworms may be "direct" or "indirect"—i.e., may or may not involve a metamorphosis. In ectoparasitic Trematodes and in some of the free-living flatworms there is a direct development, without metamorphosis; but in all the flatworms with which we are concerned the development is complicated by changes of a marked kind in the form of the young animal, and usually by one or more changes of host.

The most recent comprehensive classification of the flatworms is that of Poche,* whose arrangement of the families contained in the parasitic groups will be followed here. For the purpose of this book only two of the main classes of flatworms have to be considered. These are the Trematodes or Flukes (Class Trematoda) and the Cestodes or Tapeworms (class Cestoidea).

i. THE FLUKES OR TREMATODES (CLASS TREMATODA).

Brief Definition.—Flatworms in which the body is unsegmented (or rather unisegmental) and is without a cellular epidermis or external cilia. All members of the group are either external or internal parasites of other animals. An alimentary canal is present.

The general form of the body in the Trematodes is flattened and leaf-like as a rule, but a good many forms are stout and fleshy, some being circular, or nearly so, in transverse section. Suckers are almost invariably present on the ventral surface. These are very variable in number and arrangement.

The class is primarily divided into two orders:

(1) **MONOGENEA**, including thirteen families, which are divided by Poche into two tribes. These are chiefly ectoparasitic forms occurring on fishes and other aquatic animals. They often possess numerous suckers, or may be provided with hooks of various kinds, or a combination of hooks and suckers, for clinging to their hosts. The life-history of

* *Arch. f. Naturg.*, Abt. A., XCI., Heft 2-3 (1926).

the members of this order is direct. There may be a free-swimming, ciliated, larval stage, but this develops directly into a form like the adult, without metamorphosis or alternation of generations.

(2) **DIGENEA**, including the vast majority of the class. These forms are endoparasitic, and have an indirect life-history, complicated by metamorphosis and by the alternation of a sexual with one or more parthenogenetic generations. The Digenetic Trematodes are divided into two suborders:

(a) **Gasterostomata**, containing only one family, in which the mouth is situated in the middle of the ventral surface.

(b) **Prosostomata**, in which the mouth is at or near the anterior end. This group is subdivided by Poche into two tribes:

- (i) Fascioloidæ.
- (ii) Aspidogastroidæ.

The latter contains only a single family, and all the forms of interest in medical and veterinary helminthology belong to the tribe **Fascioloidæ**, and to one of its two subtribes (the Fascioloinæ). This subtribe contains, according to Poche, 10 "supersuperfamilies" and 60 families. Of these families only 16, belonging to 5 of the "supersuperfamilies," are of importance for our present purpose. It is proposed to deal with these groups in the order in which they are placed in Poche's system (with one exception suggested by convenience), with special reference only to those genera and species which occur in man or in the more familiar domestic animals.

In the subtribe **Fascioloinæ** the usual number of suckers is two, one being at the anterior end, and the other more posteriorly situated, either towards the middle of the body or at, or near, the posterior end. The former is known as the oral sucker, and surrounds the mouth. The other sucker, which is merely a superficial adhesive organ, is generally called the ventral sucker. The external cuticle may be smooth or may be wholly or partly covered with spines or "scales," the latter being merely flattened spines.

The alimentary canal usually consists of a relatively short, median, anterior portion and two longer, blind-ended posterior tubes which arise by the bifurcation of the former. The anterior portion may or may not show some degree of differentiation into regions. A muscular sucking-bulb, known as a pharynx, may be present in its course. The region in front of this, when it does not immediately adjoin the oral sucker, is called a pre-pharynx, while the region between it and the bifurcation of the gut is called an œsophagus. The two posterior branches, or cæca, are, in the majority of forms, simple tubular structures, but in certain families

and genera they may give off lateral branches, while in certain groups they exhibit the peculiarity of fusing together secondarily in the posterior region of the body.

The nervous system consists of several (at most eight) longitudinal nerve-cords running from the "brain" posteriorly throughout the body, and connected at intervals by transverse commissures. There appear to be no organs of special sense connected with the nervous system. The excretory organs consist usually of a single, median, more or less well-developed "bladder" (which may be sac-like, elongated, or branched at its inner end to form a Y), opening by a pore at or near the posterior end of the body, and a system of ramifying ducts whose finest capillary branches end in flame-cells distributed on a regular plan throughout the parenchyme.

With the exception of the Schistosomatidæ, all the Fascioloinæ are hermaphrodite. There are usually two testes (though in exceptional cases there may be only one, or more than two), and invariably a single ovary. The testes and ovary may be smooth-contoured, or indented or divided into a number of lobes ("lobate"), or even so deeply lobate as to be called "branched." A pair of *vasa efferentia* carry the spermatozoa from the testes, and join to form a common *vas deferens*, which opens at the genital pore, with or without a fleshy cirrus and a cirrus-sac. The terminal portion of the *vas deferens*, or ejaculatory duct, may be provided with glandular cells, and is then known as a *pars prostatica*. There may also be one or more dilatations in the course of the *vas deferens*, forming reservoirs for spermatozoa. Such a dilatation is called a *vesicula seminalis*. It may occur on the portion of the *vas deferens* which is within the cirrus-sac (*vesicula seminalis interna*), or outside it (*v.s. externa*). The *pars prostatica* may also be either inside or outside the cirrus-sac.

In connection with the oviduct there is frequently an expanded reservoir for spermatozoa (*receptaculum seminis*), and this duct is, in most forms of this group, connected with the exterior on the dorsal surface by a narrow canal (Laurer's canal) whose function is problematical, and which may represent the *genito-intestinal canal* found in some of the Monogenea. There is also, as a rule, a group of glandular cells known as a *shell-gland*. The portion of the oviduct into which these glands open is sometimes called the *oötype*. The vitelline glands are paired, but that of each side generally consists of numerous follicles whose individual ducts join to form a common duct, the two main ducts opening into the oviduct in the neighbourhood of the shell-gland. The uterus is usually a wide, convoluted tube, and is a continuation of the oviduct. It may occupy a large portion of the body with its numerous coils, or may be comparatively restricted. The fertilized eggs, just before passing

into the uterus, are thus provided with the products of the yolk-glands (yolk-cells) and of the shell-gland. Distally the uterus opens to the exterior, usually close to the opening of the male duct, and frequently the two ducts open together into a *genital atrium*.

The egg-shells of the Digenea are almost invariably provided with a detachable lid or *operculum* at one pole, which opens to allow of the escape of the embryo. The embryo, when fully formed, is covered with cilia, with which it is able to propel itself in water, and is known as a *miracidium*. It is generally provided with one or more eye-spots near the anterior end, and with a protrusible terminal papilla which serves as a boring organ in penetrating into the intermediate host. On finding themselves near the appropriate host (usually a particular species of snail) the miracidia swarm round it, apparently impelled by an irresistible attraction, and proceed to bore their way between the cells of its skin and penetrate into its interior. They usually take up a position in the pulmonary sac, liver, or some other special organ, where each, having previously lost its external coat of ciliated epithelium, develops into a simple or branching sac-like body known as a *sporocyst*. By a process of budding from the internal lining of cells, the sporocyst gives rise to "germ-balls" which develop, as a rule, into another stage, known as the *redia*. The redia is cylindrical in shape, with an annular swelling towards the anterior end and a pair of blunt processes near the posterior end. At the anterior extremity there is a mouth, leading into a muscular pharynx and a simple sac-like intestine. There is a system of excretory vessels. From the internal wall of the redia cells are budded off, frequently from a special region or from a central "rhachis" at the posterior end, and give rise either to another generation of rediæ or to the next stage, called *cercariæ*. A "birth-pore" may be formed in the wall of the redia behind the circular thickening, through which the cercariæ escape. In some groups the cercariæ develop in the sporocyst, without the interposition of a redia stage.

The cercaria is usually formed of two distinct portions, a body, more or less resembling in appearance that of the adult fluke, and a long tail. In many cases it bears a striking resemblance to a minute tadpole. The sucker or suckers of the adult appear for the first time in the cercaria, and there is a mouth, a bifid intestine, and usually a pharynx. Eye-spots may be present or absent, and flame-cells and excretory vessels are present and show a definite arrangement which appears to be characteristic for each group. Those forms which are provided with well-developed tails are generally able to swim more or less actively with them. They may make their way out of the host, and lead a free existence in water or on wet vegetation for a short time. In this case, sooner or later,

they either come to rest on vegetation or other objects and, losing their tails, secrete a protective cyst round themselves, or make their way, actively or passively, into a new host. The cercariæ of some forms, however, become encysted among the tissues of the host in which they originated, and await its ingestion by the final host. In other cases the



FIG. 1.—*Fasciola hepatica*: EGG.



FIG. 2.—*Fasciola hepatica*: EGG CONTAINING MIRACIDIUM.

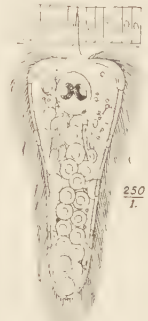


FIG. 3.—*Fasciola hepatica*: MIRACIDIUM.

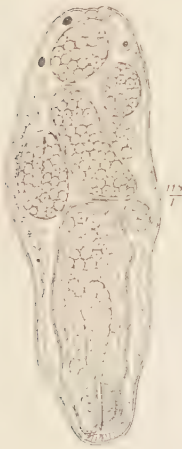


FIG. 4.—*Fasciola hepatica*: SPORO CYST.

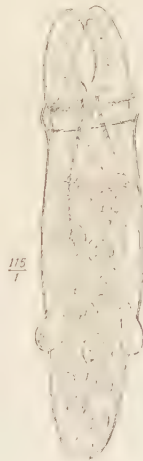


FIG. 5.—*Fasciola hepatica*: REDIA.



FIG. 6.—*Fasciola hepatica*: CERCARIA.

(FROM CASTELLANI AND CHALMERS, AFTER THOMAS.)

cercaria, upon its host being swallowed by a second animal, becomes encysted in the latter's tissues or lies free and unencysted in its body-cavity. The first intermediate host of many species is a snail, the second a fish, and the tailless, encysted cercariæ in the second host may begin to develop genital organs and are known as *metacercariæ*. Development

to sexual maturity, however, does not take place in such cases until the second intermediate host is devoured by a suitable final host, usually a vertebrate. In exceptional cases (*Schistosomatidæ*) the cercariæ, upon escaping from the final host, have the power of penetrating directly through the skin of the final, or definitive (vertebrate), host.

The following table of the principal forms of *Cercariæ* met with among the Digenetic Trematodes, and the names applied to them, is taken from Lühe:*

A. *Cercariæ* separate.

I. Tail well developed.

- (a) Body retractile within a chamber formed in the basal part of the tail.....*Cystocercous*.
- (b) Body not retractile within the tail.

1. Tail not forked.

(a) Tail without bristles.

- (i) The tail, when contracted, may be as wide as, or wider than, the body
Rhopalocercous.

- (ii) Tail always considerably narrower than the body.....*Leptocercous*.

(β) Tail with bristles (marine forms)

Trichocercous.

2. Tail forked at the tip.....*Furcocercous*.

II. Tail stumpy or absent.

- (a) A stumpy tail present.....*Microcercous*.
- (b) Tail not developed.....“*Cercariæum*.”

B. *Cercariæ* joined by their tails into a kind of colony (marine forms).....“*Rat-king Cercariæ*.”

The cercariæ of most of the forms dealt with here belong to the “leptocercous” group, in which the tail is simple and without bristles. They may or may not be provided with a boring stylet anteriorly. In the former case they are called *Xiphidiocercariæ*, in the latter *Gymnocephalous cercariæ*.

Upon the cercaria being swallowed by the proper final host, the cyst (if present) is rapidly dissolved by digestive action, and the young fluke proceeds to seek out its particular habitat, where it rapidly grows to maturity. The precise route of migration by which the ultimate habitat is reached is known only in a few cases. Forms which inhabit the alimentary

* In Brauer, *Die Süßwasserfauna Deutschlands*, Heft 17 (1909).

canal are probably protected against the action of the digestive juices by special secretions of their own, and are probably able to settle down at once in the region of their choice. In other cases there is sometimes a more or less complicated course of migration, by way of the blood-vessels or otherwise. In the case of the common liver-fluke (*Fasciola*) it has been found by Ssinitzin that the young flukes leave the alimentary canal immediately after the dissolution of their cysts, by burrowing through its walls, and migrate through the abdominal cavity, feeding here and there by attaching themselves to the viscera, until they reach the liver, which they enter by burrowing through its capsule from outside, and not (as was formerly supposed) by creeping up the bile-ducts from the lumen of the intestine.

LEPODERMATIDÆ.

The family **Lepodermatidæ** consists of small or medium-sized flukes, usually of oval form and somewhat tapering at each end. The cuticle is generally armed with small scales or spines. A pharynx and an œsophagus are present. The intestinal cæca are simple and unbranched, and usually extend almost to the posterior end of the body. The excretory bladder is Y-shaped. The genital opening is usually in or near the middle line of the body, but sometimes much displaced laterally. A cirrus-sac is present. The testes are situated near the middle of the body, one directly or obliquely behind the other, or sometimes symmetrically opposite to each other. The ovary is in front of the testes, usually towards one side of the body. The vitelline glands are well developed, and are situated at the sides of the body. The adult forms occur mainly in the alimentary canal of Amphibia, reptiles, birds and bats, while in some cases the late larval stages (encysted metacercariæ) are known to occur in insects. The family contains about thirty-five genera, of which only two need be considered in detail here.

In the genus **Lepoderma** Looss, 1899 (*-Plagiorchis* Lühe, 1899) the body is somewhat elongate and usually tapering at each end. The œsophagus is very short or absent. The genital pore is situated a little in front of the ventral sucker, usually slightly to the left of the middle line of the body, and some distance behind the bifurcation of the intestine. The cirrus-sac runs round the ventral sucker on the right side, and extends beyond it to a greater or less distance posteriorly. The testes are rounded or oval, and are placed obliquely one behind the other, with the ascending and descending branches of the uterus passing between them. The ovary is rounded and lies near the posterior end of the cirrus-sac. The vitellaria are composed of numerous closely crowded

follicles, and usually extend towards the middle line on the dorsal side of the intestinal branches. The adults of different species of this genus occur in the small intestine of members of all groups of vertebrates except fishes. The encysted cercariæ occur, so far as is known, in insects.

The species parasitic in mammals occur chiefly in bats. One, however, *L. massino* (Petrov and Tichonov, 1927), has been found in the

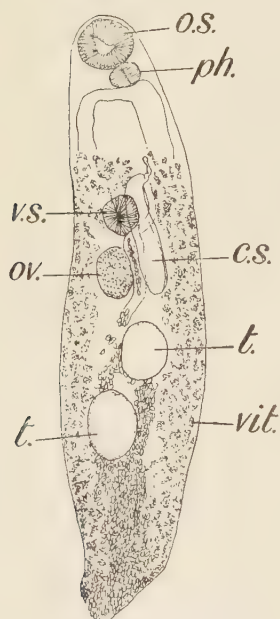


FIG. 7.—*Lepoderma massino*:
VENTRAL VIEW. (AFTER
PETROV AND TICHONOV.)

c.s., cirrus-sac; o.s., oral sucker;
ov., ovary; ph., pharynx; t., t.,
testes; vit., vitellaria; v.s.,
ventral sucker.

dog and cat in Kasakstan and Armenia. This is a small worm measuring about 1.75 to 3.1 mm. in length and 0.48 to 0.86 mm. in width. The oral sucker is about 0.15 to 0.28 mm. in diameter, the ventral sucker 0.12 to 0.18 mm., and the pharynx 0.096 to 0.16 mm. The cirrus-sac is 0.53 to 0.84 mm. in length. The vitellaria extend from a little in front of the ventral sucker (where they are confluent in the middle line) to the posterior end of the body. The coils of the uterus extend nearly or quite to the posterior end. The eggs measure about 0.035 to 0.037 × 0.021 to 0.027 mm.

Lepoderma arcuatum (Strom, 1924) is recorded from the oviduct of the fowl in Russia. This species measures 4 to 4.75 mm. in length and 1.2 to 1.5 mm. in width. The body is thick, and armed (at least on the sides) with spines, which extend as far back as the posterior limit of the posterior testis. The oral sucker is 0.461 to 0.477 mm. in diameter, the ventral sucker 0.476 to 0.492 mm., and the pharynx 0.215 to 0.261 mm. There is no œsophagus. The testes are almost globular,

and lie in the posterior half of the body. The cirrus-sac contains two vesiculæ seminales, the anterior of which is rounded, the posterior elongate. The vitellaria extend from behind the pharynx to the posterior end, and are confluent both anteriorly and posteriorly. The uterus extends only to the anterior limit of the posterior testis. The eggs measure 0.0353 to 0.0424 × 0.0212 to 0.023 mm., or occasionally as much as 0.046 × 0.0283 mm.

Lepoderma potanini (Skrjabin, 1928) occurs in the intestine of the duck in Siberia. The worm measures 1.77 mm. in length and 0.47 mm. in width. The oral sucker measures 0.158 × 0.136 mm., and the ventral sucker is 0.136 mm. in diameter. The cirrus-sac is 0.454 mm. long, and

extends posteriorly beyond the ovary. The vitellaria are arranged as in the preceding species. The eggs measure 0.032×0.018 mm.

Prosthogonimus Lühe, 1899 (= *Prymnaprion* Looss, 1899), contains a number of species parasitic in the bursa Fabricii of birds, and several of these occur in domestic poultry. Compared with other members of the family, these flukes have a relatively broad, flattened body, the greatest width of which is considerably behind the middle. The cuticle is spiny. The œsophagus is rather long. The excretory bladder has a short stem. The genital ducts open close to the anterior end, on the left side of the oral sucker. The cirrus-sac is long and cylindrical. The testes are symmetrically placed, behind the ventral sucker, and are usually irregular in shape. The ovary is dorsal to or immediately behind the ventral sucker, and is deeply lobed. The vitelline glands are situated at the sides of the middle region of the body. The coils of the uterus occupy the space between the testes, and most of the posterior region.

One species, **P. intercalandus**, Hieronymi and Szidat, 1921, which occurs in Germany, is the cause of a fatal disease in fowls, due to inflammation of the oviduct, which leads at first to the laying of abnormal (soft-shelled or shell-less) eggs, and later to peritonitis. The metacercaria of this form has been found by Szidat in the body-cavity of a dragonfly (*Libellula quadrimaculata*), and infection is acquired by the fowls in eating the intermediate host.* The adult form of this species is about 4.8 mm. long and 3.2 mm. wide. Its oral sucker measures 0.46 mm. in diameter, the ventral sucker 0.5 mm., and the pharynx 0.24 to 0.25 mm. The eggs measure 0.029×0.015 mm. The adult flukes live in the bursa Fabricii and oviduct of the host.

Prosthogonimus ovatus (Rudolphi, 1803) also occurs in the bursa Fabricii of the fowl, goose, and various wild birds. Its length is 3 to



FIG. 8.—*Prosthogonimus cuculatus*: VENTRAL VIEW. (AFTER BRAUN, MODIFIED.)

c.s., cirrus-sac; ov., ovary; t., testis; ut., uterus; vit., vitellaria; v.s., ventral sucker.

* Similar pathological conditions, due to the same or a closely related species of *Prosthogonimus*, have been reported in ducks and fowls in the United States by Kotlán and Chandler. These authors have also shown that the intermediate hosts are dragonflies, both larvæ and adults containing the encysted metacercariæ. In the case of the American species, some of the infected dragonflies belong to the genus *Tetragoneuria*.

6 mm., and its width 1 to 2 mm. The oral sucker measures 0.146 to 0.208 mm., and the ventral sucker is about twice as large (0.354 to 0.447 mm.). The diameter of the pharynx is 0.1 to 0.16 mm. The ovary lies dorsally to the ventral sucker, and the uterine coils are not closely packed, but form a "rosette." The eggs measure 0.022 to 0.024 $\times$ 0.013 mm. **P. cuneatus** (Rudolphi, 1809) is a larger form, measuring 5.2 $\times$ 1.7 mm. The body is almost triangular in shape, with a truncate posterior border. The ovary is situated behind the ventral sucker, and the coils of the uterus entirely fill the posterior region of the body. The oral sucker measures 0.3 to 0.4 mm., the ventral sucker being twice as large. The pharynx has a diameter of 0.2 mm. The eggs measure 0.023 to 0.027 $\times$ 0.013 to 0.016 mm. The adult occurs in the bursa Fabricii of the fowl, guinea-fowl, peafowl and swan, besides a number of wild birds. **P. pellucidus** (v. Linstow, 1873) is a still larger species, measuring 9 $\times$ 4 to 5 mm. It occurs in the bursa Fabricii and oviduct of the fowl, and also in the curlew (*Numenius arquatus*). A further species described from the bursa Fabricii of the fowl is *P. brauni* Skrjabin, 1919.

In the bursa Fabricii of ducks several related forms occur. **Prosthogonimus anatinus** Markow, 1902, is a small species (2.4 to 2.8 $\times$ 1.1 to 2 mm.) with oval testes, and with the male genital duct opening on a papilla near the anterior border of the oral sucker. It occurs in the domestic duck in Russia, as does also **P. rudolphii** Skrjabin, 1919, in Russia and Indo-China. This is a larger form (5.78 to 6.0 $\times$ 1.79 to 2.0 mm.). **P. skrjabini** Zakharow, 1920, is also recorded from the duck, while a closely related genus, **Schistogonimus**, is represented in ducks by **S. rarus** (Braun, 1901). This genus differs from *Prosthogonimus* in having the vaginal pore rather widely separated from the opening of the cirrus-sac.

Specimens of *Prosthogonimus* occasionally occur in the eggs of fowls, having been included at the time of formation of the shell. The species most commonly recorded is *P. ovatus*. *P. japonicus* Braun, 1901, has been found in fowls' eggs in Japan and China, and is also recorded from the oviduct of the duck in China.

DICROCELIIDÆ.

The **Dicrocoeliidæ** are small or medium-sized flukes with a more or less elongate, flattened, translucent, not very muscular body. A pharynx and an œsophagus are present. The intestinal cæca are simple and do not quite reach to the posterior end of the body. The excretory bladder is usually sac-like. The genital pore is situated in the middle line, between the oral and ventral suckers. The cirrus-sac is small. The testes

are placed opposite to each other or one behind the other behind the ventral sucker, and the ovary is behind them. The vitelline glands are well developed, and are lateral to, or partly overlap, the intestinal cæca. The coils of the uterus occupy most of the region behind the genital glands. The adult forms are parasitic in the gall-bladder and bile-ducts of vertebrates. The larval stages occur, so far as is known, in molluscs. The family contains about nineteen genera, three of which have representatives occurring in man or domestic animals.

Dicrocœlium (Dujardin, 1845) E. Blanchard, 1847, has an elongate body, more attenuated in front than behind, and with its greatest width behind the middle. The cuticle is smooth. The testes are slightly lobate and are obliquely arranged, immediately behind the ventral sucker. The ovary lies near the middle line. The species of this genus occur chiefly, if not entirely, in mammals and birds.

Dicrocœlium dendriticum (Rudolphi, 1819) (synonyms: *D. lanceolatum*, *D. lanceatum*) occurs in the bile-ducts of the sheep, ox, goat, pig, donkey, dog, and occasionally man, besides the hare and rabbit. It has a wide geographical distribution. When present in large numbers it may produce cirrhosis of the liver, like the larger liver-fluke, *Fasciola hepatica*. The worm is about 4 to 9 mm. long and 1.5 to 2.5 mm. wide. The oral sucker measures 0.3 to 0.4 mm. in diameter, the ventral sucker 0.4 to 0.45 mm., and the pharynx 0.12 to 0.13 mm. The cirrus-sac is 0.5 to 0.6 mm. long. The eggs measure 0.038 to 0.045 × 0.022 to 0.030 mm. The intermediate host of this fluke, in Europe, is possibly a fresh-water snail (*Planorbis marginatus* or *P. complanatus*), or a slug (*Arion* or *Limax* sp.), but the life-history has not yet been elucidated.* In China and the Philippine Islands the intermediate host is said to be *Planorbis umbilicatus*.

A closely related form, **Dicrocœlium hospes**, was described by Looss in 1907 from the gall-bladder of cattle from the Sudan. This species is of more uniform width than *D. dendriticum*, and has vitelline glands of very restricted extent. It measures 7 to 9 mm. in length and 1.2 mm. in width. The oral sucker is 0.33 to 0.35 mm. in diameter, the ventral sucker



FIG. 9.—*Dicrocœlium dendriticum*. (FROM CASTELLANI AND CHALMERS, AFTER LOOSS.)

a, adult worm, ventral view, magnified; b, natural size; c, egg.

* Nöller has recently suggested that a cercaria found in *Pisidium fontinale* in Germany may be that of this species.

0.38 mm., and the pharynx 0.1 to 0.11 mm. The eggs measure 0.035 to 0.04 × 0.025 mm.

Dicrocoelium macrostomum Odhner, 1911, occurs in the gall-bladder and bile-ducts of the guinea-fowl (*Numida ptilorhyncha*) in Egypt. This species measures about 4 × 1 to 1.5 mm. The oral sucker is 0.28 to 0.33 mm. in diameter, the ventral sucker 0.19 to 0.23 mm., and the pharynx 0.07 to 0.09 mm. The eggs measure 0.04 to 0.043 × 0.026 mm.

The genus **Platynosomum** Looss, 1907, closely resembles *Dicrocoelium*, but the maximum width of the body is usually in the middle or in the anterior half, and the testes lie opposite to each other at the same transverse level, immediately behind the ventral sucker. The species of this genus occur mostly in birds, but two have been recorded from domestic mammals.

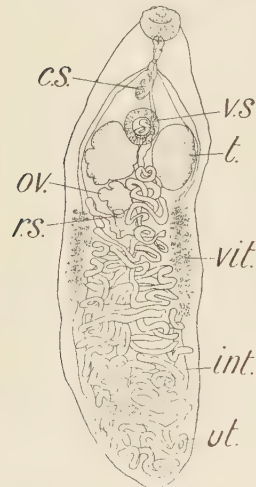


FIG. 10.—*Platynosomum fastosum*: VENTRAL VIEW. (ORIGINAL.)

c.s., cirrus-sac; int., intestinal caecum; ov., ovary; r.s., receptaculum seminis; t., testis; ut., uterus; vit., vitellaria; v.s., ventral sucker.

Platynosomum fastosum Kossack, 1910, originally described from a wild cat, *Felis minuta*, in the Königsberg Zoological Garden, has since been found to occur fairly commonly in the liver of domestic cats in British Guiana, Brazil and the Malay States. The worm measures 4 to 8 mm. in length and 1.5 to 2.5 mm. in width. The diameters of the oral and ventral suckers respectively are 0.34 to 0.5 mm. and 0.4 to 0.6 mm. The diameter of the pharynx is 0.1 to 0.15 mm. The genital opening is at the level of the intestinal bifurcation, and the cirrus-sac measures 0.4 to 0.6 × 0.15 mm. The eggs measure 0.034 to 0.05 × 0.02 to 0.035 mm.

Another species, *Platynosomum arietis*, was described by Travassos in 1918 from the small intestine of a sheep in Brazil. Its measurements appear to be very similar to those of *P. fastosum*, but it differs from that form in having almost spherical testes.

The genus **Eurytrema** Looss, 1907, consists of forms with a rather thick and broad body. The cuticle is armed with scales or spines, which appear to be easily lost. At the anterior end there is a small, fairly distinct, triangular portion bearing the oral sucker. The suckers are very large and prominent, the oral sucker being subterminal. The pharynx is relatively small. The excretory bladder is T-shaped, the transverse arms giving off anterior and posterior longitudinal branches which lie laterally

to the simple intestinal cæca. The testes are situated opposite to each other at the level of the posterior border of the ventral sucker, or even at the sides of the sucker. The genital pore is a little behind the bifurcation of the intestine. The cirrus-sac is cylindrical, and usually reaches backwards beyond the anterior margin of the ventral sucker. The genus contains a number of species occurring in mammals, birds and reptiles. The life-history is apparently unknown.

Several forms found in ruminants have been described as distinct species, but it is extremely difficult to determine how many of them should be so regarded, or whether several of them do not represent merely varieties or local races of a single species. There is considerable divergence of opinion as to whether the two best-known forms, *Eurytrema pancreaticum* (Janson, 1889) and *E. cœlomaticum* (Giard and Billet, 1892), which were regarded by Looss as distinct species, represent more than individual variations within a single species. Ware, in 1923, made a special study of a large amount of material from this point of view, and came to the conclusion that the worms were so variable that the supposed specific distinction could not be maintained.

E. pancreaticum is recorded from the pancreatic ducts of the ox, buffalo, sheep and goat, and is said to occur in Japan, China and Brazil. It measures, according to those who consider it a distinct species, 9.5 to 16 mm. in length and 5.5 to 8.5 mm. in width. The oral sucker is 2.1 mm., the ventral sucker 1.45 to 1.9 mm., and the pharynx 0.54 mm., in diameter. The eggs are of a deep brown colour, and measure 0.05×0.034 mm. The vitelline glands, according to Looss, are arranged in ten to twelve groups on either side of the body. **E. cœlomaticum** has, according to Looss, smaller suckers (both varying from about 0.83 to 0.85 mm. in diameter), placed relatively nearer together than in *E. pancreaticum*, while its vitelline glands are in only six to eight groups on each side. The eggs measure 0.042 to 0.046×0.023 to 0.027 mm. This form is recorded from cattle in Indo-China and China. Travassos, who regards *E. cœlomaticum* as a synonym of *E. pancreaticum*, records the latter as occurring in Brazil. If, however, the two forms be distinct, it appears probable that his record refers rather to *E. cœlomaticum*.

Further forms have been described under the names of *E. parvum* Senoo, 1908 (from cattle, Bonin Island, Japan), *E. dajii* Bhalerao, 1924 (from the bile-ducts of the zebu, *Bos indicus*, Burma), and *E. ovis*

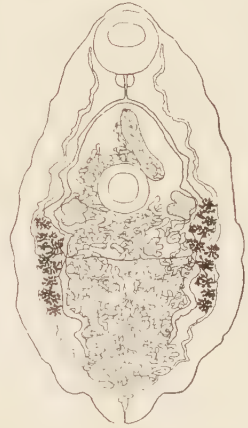


FIG. 11.—*Eurytrema pancreaticum*: VENTRAL VIEW. (AFTER LOOSS, MODIFIED.)

Tubangui, 1925 (from "native sheep," Philippines). In *E. dajii*, which is a small form (5 to 6.7×3.5 to 4 mm.), the cirrus-sac is described as not reaching the anterior margin of the ventral sucker, Laurer's canal is said to be without an external opening, and the eggs measure only 0.032 to 0.04×0.022 to 0.027 mm. *E. ovis* occurs, according to Tubangui, in an unusual situation in the host (in fat surrounding the rectum), and has the testes at the sides of the ventral sucker. Its measurements are, on the whole, in fairly close agreement with those given for *E. pancreaticum*.

OPISTHORCHIDÆ.

The members of the family **Opisthorchidæ** are small or medium-sized flukes with a flattened, translucent body, usually more or less lancet-shaped. The suckers are generally close together and not very powerful. A pharynx and a short œsophagus are present. The intestinal cæca extend almost to the posterior end. The excretory bladder is Y-shaped, with a long stem and short branches. The genital pore is immediately in front of the ventral sucker. There is no cirrus-sac. The testes are near the hinder end of the body, rounded or lobate, and placed more or less obliquely one behind the other. The ovary is a little in front of them. The vitelline glands are lateral to the intestinal cæca, and the coils of the uterus are mainly in front of the ovary.

The adult worms occur in the gall-bladder and ducts of vertebrates, and the early larval stages, so far as they are known, occur in molluscs, the later larvæ in fishes. There are about thirteen genera.

Opisthorchis R. Blanchard, 1895, is a genus comprising rather small forms in which the body is tapering anteriorly, and the testes, which are obliquely placed on either side of the median line, are usually somewhat lobed, the anterior testis generally having four lobes, the posterior five. The stem of the excretory bladder passes in a sinuous manner between the testes. The adults occur in mammals and birds, and the metacercariæ are encysted in the skin and connective tissues (especially the subcutaneous tissues) of fishes.

The typical species, **O. felineus** (Rivolta, 1884), lives in the bile-ducts, and sometimes in the pancreatic ducts, of man, the dog, cat, fox, glutton and pig. It is widely distributed in Europe and Asia. The animal measures 7 to 12×2 to 2.5 mm., and is very transparent and somewhat reddish when fresh. The eggs measure 0.026 to 0.03×0.011 to 0.015 mm. The first intermediate host is perhaps *Dreysensia polymorpha*, *Limnæa stagnalis*, or a species of *Bythinia*, according to locality. The second intermediate hosts, according to the experiments of Askanazy and of Ciurea, are the roach (*Leuciscus rutilus*), tench (*Tinca tinca*) and ide (*Idus melanotus*).

Opisthorchis viverrini (Poirier, 1886) is a form closely related to *O. felineus*, whose normal host appears to be the civet cat, but which occurs also in man in Siam. **O. noverca** (Braun, 1902), which occurs in the bile-ducts of man in India, is also extremely similar to *O. felineus*, but was referred by Barker in 1911 to a distinct genus, *Amphimerus*, on the ground that the vitelline glands showed a distinct division into pre- and post-ovarian portions on each side. **O. caninus** Barker, 1911, from the liver of the dog in India, has also been referred to a different genus, *Paropisthorchis* Stephens, 1912. This is said to differ from *Opisthorchis* in possessing a retractile ventral process on which both the ventral sucker and the genital pore are situated. Leiper, who examined a number of flukes from Indian dogs, concluded that the characters upon which these genera had been based were subject to too much variation to be reliable. "My considered opinion," he states, "is that there is but one species *Opisthorchis noverca* common to dog and man; the infection in man being an accidental one."

Opisthorchis wardi Wharton, 1921, from the cat in Luzon, Philippines, is said to differ from *O. felineus* in certain characters, but it seems possible that it may be only a variety or local race of that form. *O. [Amphimerus] pseudo-felineus* (Ward, 1901), from the cat and *Canis latrans* in North America, is a much more elongate form, sometimes measuring as much as 22 mm. in length, and appears to be quite distinct.

Opisthorchis simulans Looss, 1896, originally recorded from *Pernis apivorus*, has also been recorded from the duck. The form occurring in the duck measures 14 to 16 × 1 to 1.5 mm., and was regarded by Kowalewsky as a distinct variety.

Clonorchis Looss, 1907, closely resembles *Opisthorchis* in many respects, but may be distinguished by the fact that the testes are situated one behind the other in the middle line, and are much branched, their branches extending laterally beyond the intestinal cæca.* The excretory

* Morgan (1927) has pointed out that in different species of *Opisthorchis* there is much variation in the degree of branching of the testes, and considers *Clonorchis* a synonym of *Opisthorchis*.

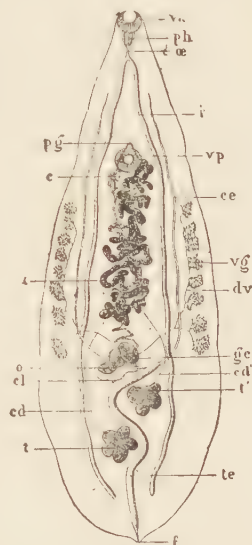


FIG. 12.—*Opisthorchis felineus*: VENTRAL VIEW. (FROM NEUMANN, AFTER RAILLIET.)

c., vas deferens; cd., cd', vasa efferentia; ce., excretory canal; cl., Laurer's canal; dv., vitelline duct; f., excretory pore; gc., ovary; i., intestinal cæcum; g., oesophagus; p.g., genital pore; ph., pharynx; t, t', testes; te., stem of excretory bladder; u., uterus; va., oral sucker; vg., vitelline glands; vp., ventral sucker.

bladder lies dorsally to them, but is sinuous as in *Opisthorchis*. A peculiar feature of the eggs is that the shell has prominent "shoulders" at the point of attachment of the operculum.

Clonorchis sinensis (Cobbold, 1875), the cause of "Asiatic liver-fluke disease," is widely distributed in the East from the east coast of India to Japan. It occurs in the bile-ducts, and sometimes in the pancreas and duodenum, of the dog, cat and pig, as well as of man. It may reach

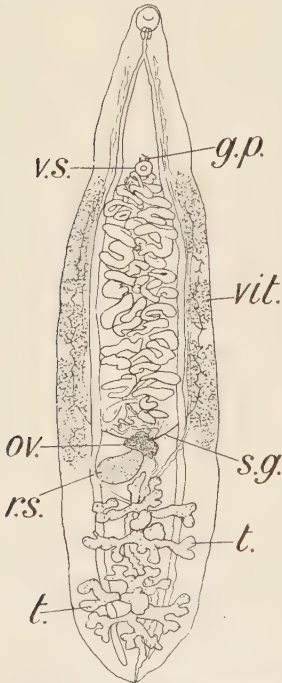


FIG. 13.—*Clonorchis sinensis*: VENTRAL VIEW. (AFTER LOOSS, MODIFIED.)

g.p., genital pore; *ov.*, ovary; *r.s.*, receptaculum seminis; *s.g.*, shell-gland; *t.*, *t.*, testes; *vit.*, vitellaria; *v.s.*, ventral sucker.

a length of 20 mm. and a width of 4 mm. The body is translucent and reddish when fresh, and is slightly wider behind than in front. The cuticle is spiny in young forms, but the spines appear to be easily lost. The oral sucker is larger than the ventral. The eggs measure 0.026 to 0.03×0.015 to 0.017 mm., and are almost black. They usually have a prolongation at the pole opposite to the operculum.

A smaller form, *C. endemicus* (Baelz, 1883), has been recognized as a distinct species by Looss and other authorities. It has, however, been shown by Kobayashi that numerous intermediate forms occur between this and the typical *C. sinensis*, and it is probable that the two forms are, at the most, only local races of the same species.

The first intermediate hosts of this fluke are various snails (*Parafossarulus striatulus* and its variety *japonicus*, *Bythinia fuchsiana*, *B. longicornis*, perhaps also *Melania hongkongensis* and *M. libertina*). The second intermediaries are fishes, mainly Cyprinidæ (species of *Pseudorasbora*, *Leucogobio*, *Acheilognathus*, *Sarcocheilichthys*, *Parapelecus*, etc., including the goldfish, *Carassius auratus*). According to Faust, almost every fresh-water fish examined in China has been found to be capable of acting as a host for this species. In South China the forms most commonly infected are the Chinese ide (*Ctenopharyngodon idellus*) and the "big-headed" fish (*Hypothalmichthys nobilis*), while in North China the commonest host is the knife-fish (*Hemiculter kneri*).

In the genus **Metorchis** Looss, 1899, the body is relatively short and broad, tapering slightly in front and rounded behind. The intestinal cæca reach to the extreme posterior end, completely embracing the testes

laterally and posteriorly. The testes are rounded or slightly lobate, and are placed obliquely or nearly opposite to each other at the hinder end of the body, with the ovary close in front of them. The excretory bladder is short, and its pore lies ventrally to the testes. The vitelline glands are in the middle region of the body, extending forward beyond the ventral sucker. The adults occur in mammals and birds, and the (second) intermediate hosts are apparently fishes.

Metorchis albidus (Braun, 1893) is a small form which occurs in the liver and gall-bladder of the cat, wild cat and fox in Europe. It measures 2.5 to 3.5×1 to 2 mm. The oral sucker is 0.24 to 0.32 mm. in diameter, the ventral sucker 0.3 mm. or less. The eggs measure 0.027 to 0.032×0.013 to 0.016 mm. Among the intermediate hosts is apparently the roach (*Leuciscus rutilus*).

Metorchis xanthosomus (Creplin, 1846) occurs in the gall-bladder of various aquatic birds, including the domestic duck, in Europe. It measures 2.8 to 3.2×0.8 to 0.9 mm. The oral sucker is elongate, measuring 0.22×0.18 mm. The ventral sucker measures 0.169 mm., and the pharynx 0.064 mm., in diameter. The testes occupy the whole width of the posterior region of the body, and the vitelline glands extend from the anterior testis almost as far as the pharynx. The eggs measure 0.027 to 0.032×0.014 mm. A similar form, *M. orientalis* Tanabe, 1921, has been found in the duck in Japan after experimental feeding with the flesh of a fish, *Pseudorasbora parva*, which is therefore the probable intermediate host of the worm.

Parametorchis Skrjabin, 1913, closely resembles *Metorchis*, but the uterus forms a rosette round the ventral sucker, and is confined to the anterior half of the body. The vitelline glands are also confined to the anterior half. The testes and ovary are lobate, the former being placed one behind the other in the third quarter of the body, with the long, S-shaped excretory bladder winding between them. **P. complexus** (Stiles and Hassall, 1894) occurs in the cat in North America. It measures 5 to 10 mm. in length and 1.5 to 2 mm. in width. A second species, *P. noveboracensis* Hung, 1926, has been described from the cat in New York. It seems doubtful, however, whether it can be considered a distinct species.

The genus **Pseudamphistomum** Lühe, 1908, resembles *Metorchis* in many respects, but the body is relatively short and peculiarly truncate behind. The cuticle is spiny. The intestinal cæca extend to the posterior end and bend slightly inwards round the testes. These are rounded, and placed almost opposite to each other, but slightly diagonally. The ovary is rounded or kidney-shaped, and is placed some distance in front of the

testes, from which it is usually separated by coils of the uterus. The excretory pore is situated ventrally, behind the testes, in a funnel-shaped, rather sucker-like depression.

Pseudamphistomum truncatum (Rudolphi, 1819) occurs in Europe and India in the bile-ducts of the cat and dog, and possibly occasionally man, besides the fox, glutton and seals. The last-mentioned animals may be its normal hosts, and the intermediate hosts are probably fishes. The worm measures 2 to 2.25 mm. in length and 0.6 to 0.8 mm. in width. The eggs measure 0.029×0.011 mm. *P. danubiense* Ciurea, 1913, has been described as a second species parasitic in the cat. This is a smaller form, measuring only about 1 to 1.5 mm. in length and 0.47 to 0.67 mm. in width.



FIG. 14.—*Pseudamphistomum truncatum*: VENTRAL VIEW. (AFTER V. RÁTZ.)

The genus **Microtrema** Kobayashi, 1920, is represented by a single species, **M. truncatum**, described by Kobayashi from the liver of the pig in Formosa. This form, which appears to be closely related to *Pseudamphistomum*, is 12 to 13 mm. long and 4 to 6 mm. wide. The body is slightly flattened, tapering anteriorly and truncate posteriorly. The cuticle is covered thickly with spines. The suckers are small, the ventral sucker being smaller than the oral and situated behind the middle of the body. The pharynx measures 0.5×0.4 mm. The intestinal cæca extend

almost to the posterior end, passing just laterally to the testes, which are placed almost opposite to each other. The excretory bladder is Y-shaped, with long arms. The ovary lies about midway between the testes and the ventral sucker, and is lobate. A large receptaculum seminis is present. The vitelline glands are arranged in about ten groups on either side, extending from behind the testes almost to the level of the intestinal bifurcation. The coils of the uterus lie mainly in front of the ventral sucker, and do not extend behind the ovary. The genital pore is a little in front of the ventral sucker. The eggs measure 0.026 to 0.03×0.013 to 0.016 mm., and contain fully formed miracidia in the uterus.

HETEROPHYIDÆ.

The **Heterophyidæ** are mostly very small flukes, seldom, if ever, exceeding 5 mm. in length. The anterior portion of the body is relatively slender, the posterior portion usually considerably widened. The cuticle, at least on the anterior portion of the body, is covered with scales. The

ventral sucker is usually situated towards the middle of the body, at some distance from the oral sucker, and is sometimes displaced from the middle line. A pharynx and a relatively long œsophagus are present. The intestinal cæca are simple, and usually extend nearly to the posterior end. The genital opening is close to the ventral sucker, and is sometimes provided with a special genital sucker, or situated in a genital sinus. There is no cirrus-sac. The testes are rounded or slightly lobate, and lie near the posterior end of the body, either side by side or obliquely one behind the other. The ovary is in front of the testes, in the middle line or displaced laterally. The vitelline glands are mainly lateral and in the posterior region. The coils of the uterus lie chiefly between the testes and the genital pore. The eggs are usually not numerous.

The family contains about twenty-five genera. The adult forms are parasitic in the intestine of mammals and birds. The early larval stages occur, so far as is known, in snails, and the metacercariæ are found encysted in fishes.

In *Heterophyes* Cobbold, 1866, the ventral sucker is median. A genital sucker is present, situated at one side of or obliquely behind the ventral sucker, and armed with chitinoïd rodlets. The testes are round or oval, and placed side by side. The ovary may be median or displaced to the right. The vitelline glands do not extend forward much beyond the ovary.

Heterophyes heterophyes (v. Siebold, 1852) occurs in the small intestine and cæcum of man, the dog and the cat in Egypt, Japan, China, Korea and Formosa (*H. nocens* Onji and Nishio, 1915, originally found in man in Japan, is now considered identical with *H. heterophyes*). The following are the measurements of *H. heterophyes*: Length, 1 to 1.7 mm.; width, 0.3 to 0.6 mm.; diameter of oral sucker, 0.09 mm.; ventral sucker, 0.23 mm.; genital sucker, 0.15 mm., with seventy to eighty rodlets. Eggs about 0.03×0.017 mm. The intermediate hosts in which this form has been found are mullets (*Mugil cephalus*, *M. japonicus*). Onji and Nishio have obtained the form *H. nocens* experimentally in the dog, cat and rat after

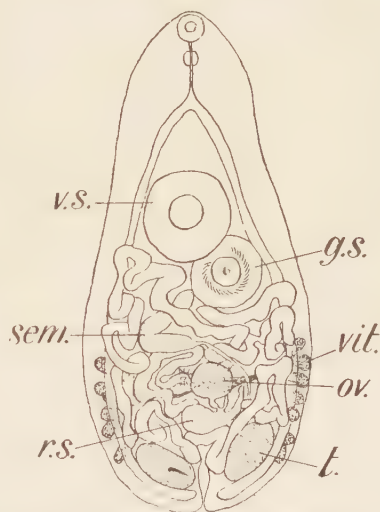


FIG. 15. *Heterophyes heterophyes*: VENTRAL VIEW. (AFTER LOOSS, MODIFIED.)

g.s., genital sucker; *ov.*, ovary; *r.s.*, receptaculum seminis; *sem.*, seminal vesicle; *t.*, testis; *vit.*, vitellaria; *v.s.*, ventral sucker.

feeding these animals on fishes of the genera *Mugil* and *Acanthogobius*. They have also more recently obtained what is considered by them to be a different form, which they have named *H. continuus*, in the cat, after feeding with *Mugil*.

Yet another form from man in Japan has been described under the name of *H. katsuradai* by Ozaki and Asada. This is a worm measuring 0.61 to 0.89 mm. in length and 0.4 to 0.55 mm. in width. The oral sucker is 0.061 to 0.063 mm. in diameter, the ventral sucker 0.195 to 0.22 mm., and the genital sucker measures 0.11 to 0.14 $\times$ 0.07 to 0.085 mm., and has fifty-two to fifty-seven rodlets. The right gut-branch is usually rather shorter than the left. The vitellaria join across the body dorsally just in front of the testes. The eggs measure 0.0253 to 0.0259 $\times$ 0.0143 to 0.015 mm. Encysted cercariæ occurring in *Mugil cephalus* have been found experimentally to belong to this species.

Two other species, *H. æqualis* and *H. dispar*, were described by Looss in 1902 in Egypt, both occurring in the small intestine of cats and dogs. Both are very small forms, less than 1 mm. in length. The ventral sucker in *H. dispar* is said to be from 0.146 to 0.168 mm. in diameter, while that of *H. æqualis* is only 0.07 to 0.09 mm. A form or variety of *H. dispar* was also recognized by Looss under the name of *limatus*. He found it once in a cat. It was more slender than the typical form, measuring 0.85 $\times$ 0.25 mm., and the ventral sucker was smaller relatively to the oral sucker. Another species, *H. persicus* Braun, 1901, was described from the Persian wolf in the Berlin Zoological Garden. It seems doubtful whether all these forms can be recognized as distinct species.

The genus **Rossicotrema** Skrjabin, 1919 (= *Cotylophallus* Ransom, 1920), has the ventral sucker well developed and median, but concealed within a genital sinus. The genital sucker, according to Ciurea, is represented only by a pair of papillæ within the sinus. The testes are oval or rounded, and obliquely placed. The ovary is to the right of the median line. The vitelline glands extend across the body dorsally in front of the genital opening, and forward as far as the intestinal bifurcation.

Rossicotrema venustum (Ransom, 1920) occurs in the intestine of the dog, cat and Alaskan fox in North America. It has a length of 1.3 mm. and a width of 0.23 to 0.65 mm. The oral sucker measures 0.04 to 0.09 mm., the ventral sucker 0.036 to 0.1 mm., and the pharynx 0.03 to 0.07 mm. in diameter. The eggs measure 0.025 to 0.035 $\times$ 0.015 to 0.02 mm. A closely similar form, **R. donicum** Skrjabin, 1919, is found in the small intestine of dogs in Russia and Roumania. According to Ciurea, the metacercariæ of this species occur in the following fishes: *Scardinius erythrophthalmus*, *Abramis brama*, and *Blicca björkna*.

Nanophyetus Chapin, 1927, represented by the species **N. salmincola** (Chapin, 1926), is peculiar in having the genital sucker feebly developed, apparently unarmed, and situated in or near the middle line, some distance behind the ventral sucker, and in the position of the testes, which are lateral to the posterior ends of the intestinal cæca.

N. salmincola, which is apparently the cause of "salmon poisoning" in dogs in certain parts of the United States, is a small worm measuring up to 0.5 mm. in length and 0.28 mm. in width. The cuticle is armed with small scales. The oral and ventral suckers are about 0.072 mm. in diameter, the pharynx about 0.04 mm. The testes are oval and lie in the posterior half of the body, with their long axes directed antero-posteriorly. The ovary is subglobular and lies to the right of, and slightly behind, the ventral sucker. The vitellaria are composed of large follicles, generally distributed over the dorsal area and at the sides of the body, and almost confluent ventrally behind the pharynx and at the posterior end. The uterus is short, lying between and behind the testes, and the eggs are few and relatively very large (0.075 to 0.085×0.055 mm.).

The adult worms inhabit the small intestine of the dog, attaching themselves to the mucosa and penetrating deeply into it. They may produce a severe ulceration, which is apparently often fatal. They have also been recorded from certain wild carnivores—the coyote (*Canis lestes*) the raccoon (*Procyon psora pacifica*) and the lynx (*Lynx fasciatus*). The serious effects of the parasite in the dog may possibly, as Chapin suggests, indicate poor adaptation to that host. The encysted metacercariæ occur in the flesh of salmon (species of *Salmo* and *Oncorhynchus*).

In the genus **Metagonimus** Katsurada, 1913 (—*Loxotrema* Kobayashi, 1912, *nec* Gabb, 1868; *Loossia* Ciurea, 1915; *Yokogawa* Leiper, 1913), the ventral sucker is situated near the right side of the body. The genital sinus is immediately in front of it, and opens together with it. The testes are obliquely placed. The ovary is median. The vitelline glands extend forward to the level of the anterior border of the ovary.

Metagonimus yokogawai (Katsurada, 1912) appears to be rather widely distributed in the Far and Near East. It has been found (and described, according to Ransom's revision, under a variety of different names) in Japan, China, Formosa, Korea and Roumania, and occurs in the small intestine of man, the dog, cat, pig and pelican. The animal measures 1 to 2.5 mm. in length and 0.42 to 0.73 mm. in width. The body is completely covered with scales. The oral sucker has a diameter of 0.048 to 0.11 mm., the ventral sucker measures 0.066 to 0.165×0.055 to 0.114 mm., and the pharynx 0.029 to 0.063×0.022 to 0.052 mm. The eggs measure 0.027 to 0.03×0.015 to 0.017 mm.

Among the first intermediate hosts of this species are said to be *Blanfordia* (*Katayama*) *nosophora*, several species of *Melania*, and *Pyradus cingulatus*. The second intermediate hosts are fishes, including the goldfish (*Carassius auratus*) and species of the genera *Cyprinus*, *Plecoglossus*, *Leuciscus*, *Acheilognathus*, *Pseudorasbora* and *Zacco*.

The following closely related forms may be briefly mentioned:

Cryptocotyle Lühe, 1899, is characterized by having both ventral and genital suckers poorly developed and situated within the genital sinus. *C. lingua* (Creplin, 1825), normally a parasite of gulls, has been found in the dog in America.

Centrocestus Looss, 1899, is very similar to the last genus, but has the oral sucker armed with chitinoid rodlets. A form has been recorded from the dog in Formosa by Leiper, who considers it a variety, *caninus*, of *C. cuspidatus* (Looss, 1896), originally recorded from the kite in Egypt. According to Faust and Nishigori, however, this is probably *Stamnosoma formosanum* (see below).

Ascocotyle Looss, 1899, is another very similar form. The species *A. minuta* Looss, 1899, has been found in the dog and cat, as well as in the heron, in Egypt, and apparently also in Brazil. *A. italica* Alessandrini, 1906, was described from the dog in Italy.

Stamnosoma Tanabe, 1922, probably belongs to the Heterophyidae, and may, according to Stiles and Hassall, possibly be a synonym of *Centrocestus*. The oral sucker is surrounded by a complete double

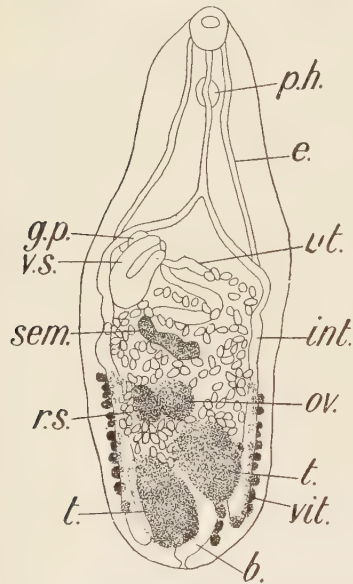


FIG. 16.—*Melagonimus yokogawai*: VENTRAL VIEW. (AFTER CIUREA.)

b., excretory bladder; e., excretory canal; g.p., genital pore; int., intestinal caecum; ov., ovary; ph., pharynx; r.s., receptaculum seminis; sem., seminal vesicle; t., testes; ut., uterus; vit., vitellaria; v.s., ventral sucker.

circle of spines. Two species, though probably normally parasites of fish-eating birds, have been described as capable of infecting man and other mammals—*S. armatum* Tanabe, 1922, in Japan, and *S. formosanum* Nishigori, 1924, in Formosa. The intermediate hosts appear to be (1) snails of the genus *Melania* and (2) Cyprinoid fishes belonging to a number of genera.

Monorchotrema Nishigori, 1924, has two species, *M. taihokui* and *M. taichui*, characterized by the presence of a single testis. Both apparently occur naturally in the night-heron (*Nycticorax*), in Formosa,

but Faust and Nishigori find that they are capable of infecting mammals, including man, dog, cat and laboratory rodents, and believe that they may occur naturally in these hosts. The life-history and intermediate hosts are similar to those of *Metagonimus* and *Stamnosoma*.

TROGLOTREMATIDÆ.

The family **Troglorematidæ** consists of forms with a fleshy but more or less flattened body, convex dorsally and flat or concave ventrally. The cuticle is spiny. The suckers are sometimes poorly developed, and a ventral sucker may be absent. A pharynx and a rather short œsophagus are present. The excretory bladder is Y-shaped or tubular. The testes are lobate or branched, elongate, and situated opposite to each other in or behind the middle of the body. The ovary is usually much lobed and placed to the right of the middle line immediately in front of the testes. The vitelline glands are usually well developed and mainly dorsal in their distribution. The adult worms occur in carnivorous mammals and in birds, frequently living in pairs in cyst-like cavities in the tissues.

In the genus **Paragonimus** Braun, 1899, containing the well-known lung-fluke, the body is more or less oval, rather thick, and has been likened to a coffee-bean in general appearance. The spines are arranged in groups. The ventral sucker lies at or in front of the middle of the body. The excretory bladder is cylindrical and very long, extending forward as far as the intestinal bifurcation. The genital pore is just behind the ventral sucker. A cirrus-sac is absent. The testes and ovary are usually deeply lobate, the ovary being laterally placed in front of the testes. The uterus forms a coil close to the ventral sucker on the side opposite to the ovary. The adults occur in the lungs of mammals, often in pairs.

Paragonimus westermanii (Kerbert, 1878) measures about 8 to 16 mm. in length and 4 to 8 mm. in width. Its colour when fresh is reddish brown. The subterminal oral sucker measures 1 to 1.4 mm. in diameter, and the ventral sucker is about the same size. The eggs measure 0.085 to 0.1 × 0.05 to 0.067 mm. The pig is probably the normal host of this form, but it, or one or other of various forms which may be merely variations of it, occurs also in the lungs, brain, etc., of man, the dog, cat, ox, goat and various wild carnivores. The geographical range of these forms is very wide, including Japan, Formosa, Korea, China, the Philippines, North and South America, New Guinea and possibly Italy.

Authorities are still divided as to the validity of various forms which have been described as distinct species of *Paragonimus*. *P. westermanii*, originally described from the tiger, and *P. ringeri* (Cobbold), from man, are considered by many to be identical. Ward has described another

form, *P. kellicotti*, from the pig, dog and cat in North America. Ward and Hirsch, in 1915, stated their opinion that the three species mentioned could be differentiated by the shape and arrangement of the cuticular spines and by certain characters of the alimentary tract. Vevers, in 1923, supported this view, finding also differences in the form of the eggs. He found, however, that there was so much variation in the internal organs that no reliance could be placed upon specific distinctions based on them. In host-range and in geographical distribution the three species referred to appear to overlap. Kobayashi, who has studied specimens from many hosts in Korea, has found the features relied upon by other

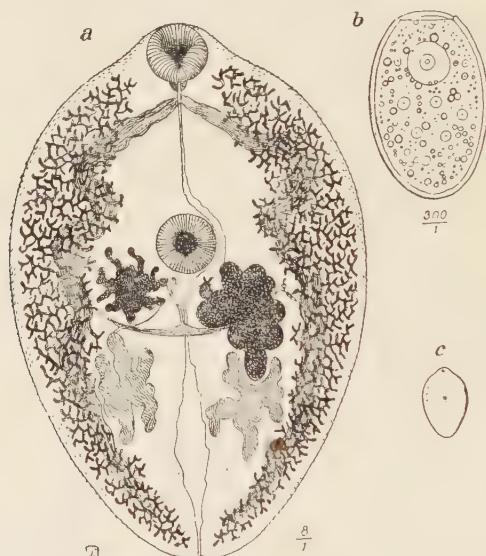


FIG. 17.—*Paragonimus westermanii*. (FROM CASTELLANI AND CHALMERS, AFTER LOOSS.)

a, adult, ventral view, magnified; *b*, egg; *c*, adult, natural size.

authors as specific characters to be extremely variable, and considers them to be merely expressions of individual variation.

The first intermediate hosts of *Paragonimus* in Japan are believed to be numerous species of the genus *Melania* (*Tiara*). The second intermediate hosts are, according to Japanese investigators, various fresh-water Crustacea: *Potamon* (*Geothelphusa*) *dehaani*, *P. obtusipes*, *P.* (*Parathelphusa*) *sinensis*, *Sesarma dehaani*, *Eriocheir japonicus*, *E. sinensis*, *Astacus japonicus*, *Astacus* (*Cambaroides*) *similis*, *A. (C.) dauricus*. In Venezuela, Iturbe and González have found the intermediaries to be (1) *Ampullaria luteostoma* and (2) *Pseudotelphusa iturbei*.

In *Collyriclum* Ward, 1917, the body is discoidal, somewhat broader than long, and of a gelatinous, translucent appearance. The musculature

is very feebly developed. The oral sucker is poorly developed, and a ventral sucker is absent. The intestinal cæca are wide. The genital pore is near the middle of the body. The testes are oval, and situated behind the ovary, which is much lobed. The vitellaria consist of few follicles and are antero-lateral in position. The uterus forms irregular coils in the posterior region of the body.

C. faba (Bremser, in Schmalz, 1831) occurs in subcutaneous cysts, especially on the abdominal surface and in the cloacal region, in birds. Its usual hosts appear to be the house sparrow, starling and a number of other passerine birds, but it has been observed on several occasions in the fowl and turkey in Europe and in North America. Cases of heavy infestation in young birds may lead to great emaciation, anæmia, paralysis and death. The name of "cutaneous monostomidosis" has been given by Marotel to an epidemic of this affection observed by him in turkeys. The cysts are 4 to 6 mm. in diameter, and each usually has a central orifice through which the eggs of the worms escape. Each cyst contains two worms, which lie with their ventral surfaces apposed, and are usually of different sizes, the smaller apparently functioning as a male while the larger acts as a female.

The worms measure 4 to 5 mm. in length and 4.5 to 5.46 mm. in width. The oral sucker is 0.2 to 0.45 mm. in diameter, the pharynx 0.11 to 0.194 mm. The ovary is T-shaped, each of its three main divisions being subdivided into from five to ten lobes. The vitellaria, which are sometimes asymmetrical, consist of six to nine groups of follicles on each side. The eggs are very small, measuring 0.019 to 0.021×0.0097 to 0.011 mm.

PHILOPHTHALMIDÆ.

The **Philophthalmidæ** are a small family containing three genera of medium-sized flukes parasitic in birds. The testes and ovary are situated near the posterior end of the body, behind the uterus, the former being considerably lobate. The genital pore is in front of the ventral sucker. The cirrus-sac is very long. The vitelline glands are tubular, and may be situated on the outer or on the inner side of the intestinal cæca. The coils of the uterus extend laterally beyond the cæca.

Philophthalmus gralli Mathis and Léger, 1910, is a worm with a yellowish, translucent, lanceolate body, tapering in front and rounded behind, occurring in the conjunctival sacs of fowls, ducks and peacocks in Indo-China. It measures 3 to 6 mm. in length and 0.9 to 1.7 mm. in width. The oral sucker is about 0.4 mm., and the ventral sucker nearly 0.6 mm. in diameter. The genital pore lies midway between the suckers. The testes are placed one behind the other. The eggs measure $0.158 \times$

0.07 mm. The infection appears in some cases to give rise to inflammation and erosion of the mucous membrane.

FASCIOLIDÆ.

The **Fasciolidæ** are large flukes with a broad, flattened body. The cuticle is typically spiny. The oral and ventral suckers are close together. A pharynx and a short œsophagus are present. The intestinal cæca are commonly much branched, especially on their outer sides. The excretory bladder is also much branched. The genital pore is close in front of the ventral sucker, and a cirrus-sac is present. The testes are placed either directly or diagonally one behind the other, and are much branched. The ovary lies in front of them, to one side of the median line, and is also branched. The vitelline glands are extremely diffuse, mainly lateral in distribution, but extending towards the middle line ventrally and sometimes dorsally as well, and meeting across the body behind the testes.

The family contains nine genera, the adult forms of which occur mainly in the liver or intestine of mammals. Two of these genera are of considerable importance in veterinary and medical helminthology. The larval stages are parasitic in snails, up to the development of the cercaria, which has a short free-living period, after which it becomes encysted on vegetation or other suitable objects, and does not require a second intermediate host.

In **Fasciola** Linnæus, 1758, the body is large and leaf-like. The anterior end frequently forms a conical portion marked off by distinct "shoulders" from the rest of the body. The cuticle is spiny. The ventral sucker is near the base of the anterior cone, and is of about the same size as the oral sucker. The intestinal cæca extend to the posterior end of the body, and have many lateral diverticula, those on the outer side being longer than those on the inner side. These diverticula frequently give off secondary branches. The genital pore is median, immediately in front of the ventral sucker. The precise arrangement of the testes is difficult to determine, on account of their complex branching, but the arrangement of the vasa deferentia appears to indicate that they are in reality diagonally placed. The uterine coils form a rosette between the testes and the ventral sucker. The eggs are large.

The usual habitat of the adults is the liver of mammals, more particularly of herbivores. Sometimes, however, they occur in the lungs and elsewhere. The life-history of *F. hepatica* (see above, p. 9), which was originally worked out very thoroughly by Thomas, has become the classical example of a Trematode life-history, and is familiar to all students of zoology, being dealt with at some length in almost every text-book.

Fasciola hepatica Linnæus, 1758, reaches a length of about 20 to 30 mm., and a width of 8 to 13 mm. The anterior "cone" is marked off by particularly prominent "shoulders." The vitelline glands extend across the body both dorsally and ventrally to the intestinal cæca. The eggs measure about 0.13 to 0.145 $\times$ 0.07 to 0.09 mm.

This species has a cosmopolitan distribution, and occurs in the sheep, ox, goat, buffalo, camel, llama, pig, horse and donkey, besides a number of wild ruminants, rodents and even the kangaroo. A number of cases of human infection have been recorded. In some of these the parasites were "erratic"—i.e., they occurred in blood-vessels or in various tissues and organs other than the usual habitat. *L. hepatica* is responsible annually for the death of large numbers of sheep from the disease known as "liver-rot."

It is probable that the geographical range of the species has been largely extended by human agency, as it occurs almost wherever sheep have been imported, and seems everywhere to have been able to find some intermediate host in which it can complete its life-cycle. The only snail which is definitely known to act as an intermediate host throughout Europe, and as far eastwards as Tibet, is *Limnæa truncatula*. In North America the intermediate host may be *Limnæa humilis* or *Physa fontinalis*; in Venezuela *Ampullaria luteostoma* has been incriminated, while another South American host is possibly *Limnæa viator*. *Limnæa oakusensis* and *L. rubella* are said to act as hosts in the Sandwich and Hawaiian Islands, *L. tenasiatrus* in Australia, *L. pervia* and *L. japonica* in Japan, and *L. natalensis* and *Isidora tropica* in South Africa.

The place of *F. hepatica* is taken throughout a large part of Africa* by another species, *F. gigantica* Cobbold, 1855. In some places, however, the two forms both occur. *F. gigantica* is distinguishable by its larger



FIG. 18. — *Fasciola hepatica*: VENTRAL VIEW. (AFTER SOMMER, MODIFIED.)

c.s., cirrus-sac; int., anterior portion of intestine; ov., ovary; t., t., branches of testes; vit., vitellaria; v.s., ventral sucker.

* *F. gigantica* has also been recorded from a buffalo in the Philippines, and from cattle in Burma and Korea.

size and much more elongate shape. It measures from 25 mm. to as much as 75 mm. in length, and from 3 to 12 mm. in width. This form is common in the goat, sheep, ox, zebu and buffalo, and also in some of the wild herbivores of Africa, such as the giraffe. It has occasionally been found in the lungs of man. The intermediate hosts of the species in South Africa appear to be *Limnæa natalensis* and *Physopsis africana*.

A third and very large species occurs in North America. This is *F. magna* (Bassi, 1875), which is found in the liver and lungs of cattle and

various species of deer. It has also occurred in Europe, but this was probably as the result of importation from America. The body of this fluke is flesh-coloured and very large and thick, sometimes attaining a length of 100 mm. and a width of 26 mm. The anterior "cone" is not very distinct. The vitelline glands are confined to the ventral side of the intestinal cæca. The eggs measure 0.109 to 0.168×0.075 to 0.096 mm. Ward considers that this species should be placed in a distinct genus, *Fascioloides*, on account of the distribution of the vitelline glands.

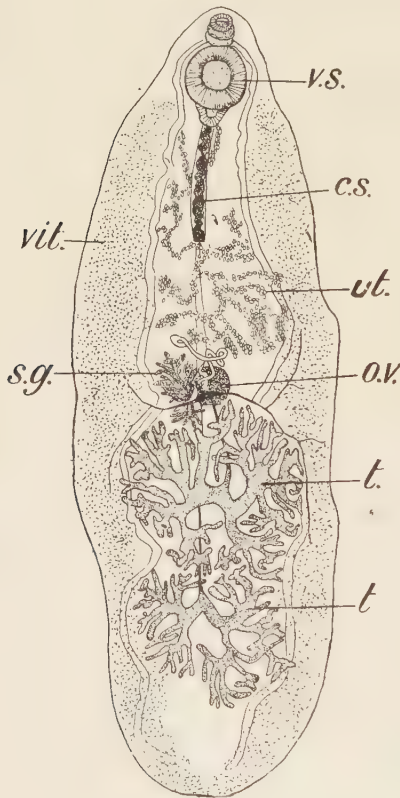


FIG. 19.—*Fasciolopsis buskii*: VENTRAL VIEW. (AFTER ÖDHNER, MODIFIED.)

c.s., cirrus-sac; o.v., shell-gland; s.g., ovary; t., t., testes; ut., uterus; vit., vitellaria; v.s., ventral sucker.

In the genus *Fasciolopsis* Looss, 1899, the body is thick and fleshy, and greyish or brownish in colour. The cuticle is spiny, but the spines are easily lost in macerated or poorly preserved specimens. The anterior region is not distinct from the rest of the body. The ventral sucker is much larger than the oral sucker, and has a posterior sac-like extension.

The intestinal cæca are unbranched and sinuous. The testes are much branched and lie one behind the other in the posterior region of the body. The cirrus-sac is very long and cylindrical. The eggs resemble those of *Fasciola*. The adult worms are parasitic in the alimentary canal of mammals,

Fasciolopsis buskii (Lankester, 1857) is common in the intestine of man or the pig (not always in both in the same locality) in India, Assam, Siam, the Malay Archipelago and China. It may also, apparently, occur occasionally in the stomach. The worm measures about 30 to 70×14 to 15 mm. The diameter of the oral sucker is about 0.5 mm., and that of the ventral sucker about 0.7×1.5 to 2 mm. The eggs are dark-coloured and measure about 0.125 to 0.14×0.075 to 0.09 mm.

No general agreement has yet been reached as to the validity of the various other species of *Fasciolopsis* that have been described (*F. rathowisi*

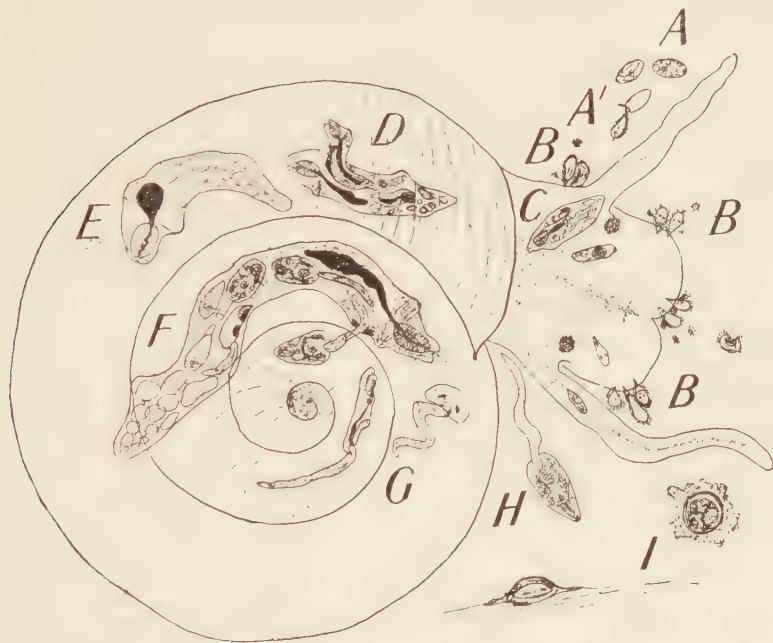


FIG. 20.—DIAGRAM OF LIFE-HISTORY OF *Fasciolopsis buskii*. (AFTER BARLOW.)

A, egg; A', miracidium escaping from egg; B, B, miracidia entering snail; C, sporocyst; D, redia, with daughter redia escaping; E, daughter redia; F, older daughter redia with cercariæ; G, cercariæ; H, cercaria escaping from snail; I, encysted cercariæ.

Poirier, 1877; *F. fülleborni* Rodenwaldt, 1909; *F. goddardi* Ward, 1909; *F. spinifera* Brown, 1917). Recent comparative studies, however, indicate that the supposed differences between these forms and *F. buskii* are to be accounted for by individual variation, degree of contraction, and the loss, in some specimens, of the cuticular spines.

The life-history of *Fasciolopsis* is similar to that of *Fasciola*, and among the intermediate hosts, according to the researches of Nakagawa and of Barlow, are *Planorbis cænosus* and *P. (Segmentina) largillierti* in Formosa, and *Planorbis schmackeri* and *Segmentina nitidellus* in China.

Barlow has given an extremely interesting account of the way in which *Fasciolopsis* infection is spread in the Chekiang Province of China. The snail hosts are particularly fond of certain plants regarded as delicacies by the Chinese and specially grown in ponds (the water caltrop, *Trapa natans*, and a plant known as *Eliocharis tuberosa*).* The snails often burrow right down into the tubers of these plants, and the cercariæ which escape from them become encysted on or in the tubers. These are eaten raw by the Chinese, and the crop is habitually fertilized by mixing human excreta, often containing the eggs of *Fasciolopsis*, with the water. Hence the conditions are such as to provide every opportunity both for the worms to multiply and for human beings to become infected.

Among the pathological effects attributed to human infection with *Fasciolopsis* are anæmia, diarrhoea and abdominal pain, followed sometimes by œdema and ascites.

BUNODERIDÆ.

The family **Bunoderidæ** is now restricted to the genus **Bunodera** Railliet, 1896. In the species of this genus the anterior portion of the body is capable of considerable elongation, forming a "neck." The oral sucker has six muscular processes. A pharynx and a long œsophagus are present. The excretory bladder is sac-like. The genital pore is situated a little in front of the ventral sucker. There is a membranous cirrus-sac. The testes are placed obliquely one behind the other in the posterior region of the body. The ovary is considerably in front of them. The vitelline glands are lateral, extending throughout nearly the whole length of the body. The uterus extends to the posterior end and occupies the region ventral to the testes. These worms are typically parasites of fishes, but one species found in the fowl has been attributed to the genus. This is **B. linearis** (Rudolphi, 1793), which was originally recorded from the large intestines of two chickens at Greifswald. The body is described as reddish, and measuring 10 to 15 mm. in length and 1.5 mm. in width. It seems possible that the infection of chickens may be merely accidental.

CYCLOCÆLIDÆ.

The **Cyclocœlidæ** (or Monostomidæ) are a group of medium-sized or rather large Trematodes whose chief peculiarity is the absence of an oral sucker. The ventral sucker is also usually absent. The body is somewhat flattened, and is rounded behind. The mouth is terminal or sub-terminal, and leads into a muscular pharynx. The two lateral branches

* Chandler (1928) reports that infection in Eastern Bengal has been traced to the eating of "water nuts known locally as 'singara' (*Trapa bicornis*), which are commonly peeled by the teeth."

of the intestine are usually simple, and are always joined together posteriorly so as to form a continuous loop. The excretory pore is dorsally situated near the posterior end. The excretory bladder is small and sac-like, and is situated between the intestinal loop and the posterior end. The genital pore is median, a little behind the mouth. There is a poorly developed cirrus-sac. The testes lie obliquely to the middle line in the posterior region of the body, and may be smooth or lobate. The ovary is a compact organ lying between the testes, or occasionally in front of them. The vitelline glands are mainly lateral to the intestinal branches. The uterus occupies with its coils, or rather transverse loops, most of the space between the intestinal bifurcation and the posterior end.

The family contains about sixteen genera, whose members occur as adult forms mainly in the body-cavity, air-sacs or nasal cavities of aquatic birds, chiefly of the families Charadriidæ and Rallidæ. A few species, however, have been recorded from domestic birds.

In the genus *Hyptiasmus* Kossack, 1911, the ovary is in a straight line with the two testes, and lies close in front of the posterior testis. The vitelline glands of both sides join posteriorly. The loops of the uterus extend laterally beyond the outer edges of the intestinal branches.

H. tumidus Kossack, 1911 (formerly recorded as *Cyclocœlum arcuatum* Brandes, but distinct, according to Kossack, from that form), occurs in the infraorbital sinus and antrum of Highmore of the goose (in Germany). This species measures 17·9 to 19·8 mm. in length and 4·14 to 4·95 mm. in width. The body is almost oblong, but somewhat rounded at each end. The eggs measure $0\cdot118 \times 0\cdot059$ mm.

In *Cyclocœlum* Brandes, 1892 (= *Monostomum* Zeder, in part), the testes and ovary form the angles of a triangle, with the ovary at the same level as, or just in front of, the posterior testis. The vitelline glands of the two sides remain distinct posteriorly, and the loops of the uterus are short, not extending laterally beyond the outer edges of the intestinal cæca. *C. mutabile* (Zeder, 1800), which is normally a parasite of the moorhen, has been somewhat doubtfully recorded from the turkey.

Typhlocœlum Stossich, 1902, is very like *Cyclocœlum*, but the testes are deeply lobed, the intestinal branches have short diverticula on the

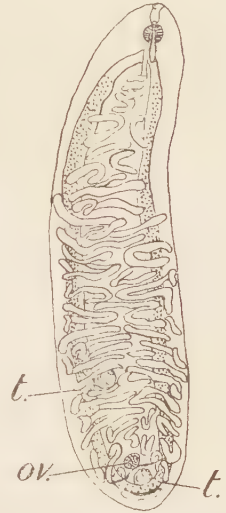


FIG. 21. —*Hyptiasmus tumidus*. (AFTER KOSSACK.)
ov., ovary; t., t., testes.

inner side, instead of being simple, and the uterine loops are confined to the space between the intestinal branches. The species **T. obovale** Neumann, 1909, was based on worms recorded by Magalhães from the trachea and bronchi of ducks at Rio de Janeiro, and said to have caused the death of the birds by suffocation. These worms measured 12×5 mm., and were wider in front than behind. The eggs measured 0.154×0.09 mm. According to Skrjabin, it is doubtful whether this species belongs to *Typhlocœlum* or to the following genus.

Tracheophilus Skrjabin, 1913, is similar to *Typhlocœlum*, but the testes and ovary are not lobate, and the ovary is at the level of the anterior testis. The vitelline glands are well developed, and consist of small follicles extending both dorsally and ventrally to the intestinal branches. **T. sisowi** Skrjabin, 1913, has been recorded from the trachea of the domestic duck in France, and from the wild duck in Russian Turkestan. It is 6 to 11.5 mm. in length and about 3 mm. in width. The eggs measure 0.122×0.063 mm.

NOTOCOTYLIDÆ.

The family **Notocotylidæ** is placed here not because the Cyclocœlidæ are considered its nearest relatives, but merely for convenience. Superficially, at least, the members of these two groups bear such a resemblance to each other that they were for some time regarded as forming a single family. The Notocotylidæ are a group of some half-dozen genera parasitic in the alimentary canal of aquatic birds and mammals. They are remarkable for the absence of a ventral sucker, and for this reason are often referred to as "Monostomes," like the Cyclocœlidæ. An oral sucker, however, is present, and a pharynx is absent. The worms usually have a somewhat elongate, flattened body, somewhat tapering in front and broad and rounded behind. The cuticle, anteriorly and ventrally, is armed with minute spines. On the ventral surface there are usually three longitudinal rows of peculiar organs consisting of groups of unicellular glands. The intestinal cæca are simple, and end separately and blindly behind, without joining into a loop as in the Cyclocœlidæ. The excretory pore is dorsally placed, near the posterior end, and the excretory bladder is Y-shaped, with a very short stem and long arms, which join again anteriorly, dorsally to the oral sucker. The genital pore is median, lying a little behind the oral sucker. There is an elongate cirrus-sac. The testes are placed symmetrically opposite to each other at the posterior end of the body, *laterally to the intestinal cæca*. The ovary lies between them. Laurer's canal is present, but a receptaculum seminis is absent. The vitelline glands are at the sides of the body, in

front of the testes. The uterus, in a series of transverse loops, extends from the testes to the posterior end of the cirrus-sac, not passing laterally beyond the intestinal cæca. The eggs are peculiar in being provided with long filaments at both poles.

In *Notocotylus* Diesing, 1839, as restricted by Odhner, the body is narrowed in front, the vagina is about half as long as the cirrus-sac, and the ventral groups of glands open into evaginable pockets. *N. attenuatus* (Rudolphi, 1809) occurs in the cæca and rectum of the duck, goose and fowl, as well as in various wild aquatic birds. This worm measures 2 to



FIG. 22.—*Catatropis verrucosa*: VENTRAL VIEW, SURFACE. (AFTER ODHNER.)

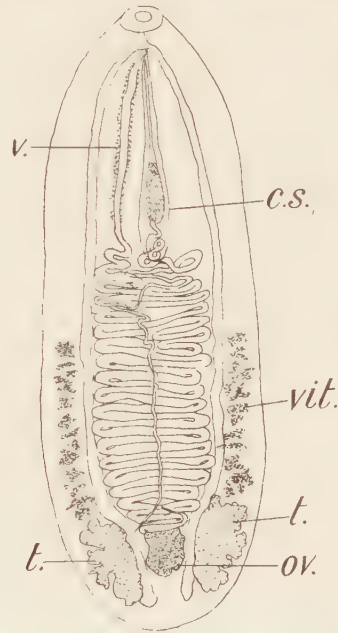


FIG. 23.—*Catatropis verrucosa*: DORSAL VIEW, SHOWING ANATOMY. (AFTER ODHNER.)

c.s., cirrus-sac; ov., ovary; t., t., testes; v., vagina; vit., vitellaria.

5 mm. in length and 0.65 to 1.4 mm. in width. The oral sucker has a diameter of 0.11 to 0.2 mm. There are, according to Odhner, sixteen or seventeen groups of glands in the lateral rows and fourteen or fifteen in the median row. The eggs (measured without the filaments) are 0.02 to 0.022 mm. long. Joyeux has shown that *Planorbis rotundatus* acts as an intermediate host for this species.

N. ægyptiacus Odhner, 1905, from the cæca of the duck in Egypt, differs from *N. attenuatus*, according to Odhner, in having only twelve to fourteen groups of glands in each row.

In the genus **Catatropis**, separated by Odhner in 1905 from *Notocotylus*, the body is almost equally rounded in front and behind. The vagina is almost as long as the cirrus-sac. The groups of glands are poorly developed, those of the middle row being situated on a keel-like ridge, according to Odhner, and those of the lateral rows opening on non-retractile papillæ. **C. verrucosa** (Frölich, 1789) occurs in the cæca of the duck, goose and fowl, besides various wild birds of the duck tribe. In this species the body measures 1 to 5 mm. in length and 0.75 to 1.25 mm. in width, the oral sucker has a diameter of 0.13 to 0.16 mm., and the eggs (without their terminal filaments) measure 0.018 to 0.02 mm. in length.

In **Paramonostomum** Lühe, 1909, the body is short and oval, with its greatest width a little behind the middle. The groups of glands characteristic of the last two genera are apparently absent. **P. alveatum** (Mehlis, in Creplin, 1846) is a form occurring in the cæca and intestine of the goose, swan and various wild ducks in North Germany. It measures 0.6 to 1.0 × 0.4 to 0.7 mm., and has an oral sucker measuring 0.05 to 0.08 mm. in diameter. The eggs (without their filaments) measure 0.019 to 0.021 × 0.008 to 0.01 mm.

ECHINOSTOMATIDÆ.

The members of the family **Echinostomatidæ** vary very considerably in size, but all have a more or less elongate, muscular body, and are readily recognized by the presence of a more or less pronounced, fleshy, kidney- or horseshoe-shaped structure surrounding the oral sucker dorsally and laterally, and bearing a single or double row of straight spines. This "head-crown," as it may conveniently be called, is not continued across the ventral surface, and its series of spines may or may not be interrupted in the middle line on the dorsal side. The cuticle of the body, at least in the anterior region, is usually provided with spines or scales. The ventral sucker is generally rather near the anterior end. A pharynx and an œsophagus are present. The intestinal cæca are simple and reach almost to the posterior extremity. The excretory bladder is Y-shaped. The genital pore is median and lies between the intestinal bifurcation and the ventral sucker. A cirrus-sac is usually present. The testes are generally in the posterior half of the body, and are placed directly or diagonally one behind the other. The ovary is in front of the anterior testis, in the median line or to the right side of it. The vitelline glands are mainly distributed along the sides of the body, but commonly extend inwards towards the middle line behind the testes. The coils of the uterus lie between the ovary and the ventral sucker. The eggs are usually relatively large.

The adults occur in the alimentary canal or bile-ducts of vertebrates, more especially of birds. The larval stages (rediae, cercariæ and encysted metacercariæ) occur, as a rule, in molluses, though in one genus there is evidence that fishes act as the second intermediate hosts. The life-cycle appears to be generally as follows: The miracidium, after hatching in water, enters a mollusc, in which it gives rise to sporocyst and redia stages. The cercariæ formed in the latter leave the snail, and proceed to enter another snail, of the same or a different species, in which they become encysted. The definitive host becomes infected by ingesting this second snail. The family contains some thirty-two genera.

The genus *Echinostoma* Rudolphi, 1809, consists of medium-sized or rather large forms with a double row of spines in the "head-crown," not interrupted dorsally. The cuticle is spiny on the ventral surface of the anterior region. The suckers are close together. The cirrus-sac is small and lies almost entirely in front of the ventral sucker. The testes are usually rounded or oval, with their long axis arranged longitudinally, and may or may not be lobed. They lie in the middle line, one immediately behind the other, in the posterior half of the body. The ovary is round or transversely oval, and situated in the middle or a little to one side. The vitelline glands do not extend forward beyond the posterior border of the ventral sucker. The adults occur in the intestine of birds.

Echinostoma revolutum (Frölich, 1802) (= *E. echinatum* (Zeder, 1803)) is a parasite of the rectum and cæca of the duck, goose, swan and fowl, besides a number of wild aquatic birds. It is 10 to 22 mm. long. The oral sucker measures 0.25 to 0.5 mm., and the ventral sucker 0.67 to 1.69 mm. in diameter. The width of the pharynx is 0.21 to 0.35 mm. The ventral surface is spiny as far back as the ventral sucker. The "head-crown" has thirty-seven (exceptionally only thirty-five) spines. The testes are extremely variable in shape. The eggs measure 0.097 to 0.126×0.059 to 0.071 mm.

The cercariæ of this species (*Cercaria echinata* v. Siebold) occur in *Limnæa stagnalis* and *Physa occidentalis*, and infection of the final hosts is due to eating these snails.

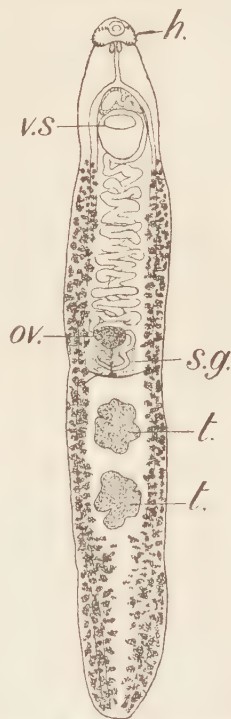


FIG. 24.—*Echinostoma revolutum*: VENTRAL VIEW. (AFTER LOOSS, MODIFIED.)

h., "head-crown"; ov., ovary; s.g., shell-gland; t., t., testes; v.s., ventral sucker.

Echinostoma paraulum Dietz, 1909, differs only in minor characters from *E. revolutum*, and it seems somewhat doubtful whether it deserves to be regarded as a distinct species. Its length is given as 4 to 7 mm., and the testes are divided by a constriction into two unequal parts. The "head-crown" is similar to that of *E. revolutum*. The range of hosts is also similar.

Echinostoma columbæ Zunker, 1925, recorded from the small intestine of the pigeon in Germany, is a form measuring 2.63 to 7.65 mm. in length and 0.85 to 1.53 mm. in width in the posterior region. The head-crown has a deep ventral indentation and bears thirty-seven spines (the two rows of marginal spines containing twenty-seven, and each group of "corner spines" five). The body is stated to be without spines. The oral sucker is 0.187 to 0.23 mm. in diameter, the ventral sucker 0.527 to 0.714 mm., and the pharynx 0.17 to 0.221 mm. The testes, in mature specimens, are divided by a constriction into two unequal portions. The vitellaria are confined to the lateral areas. The eggs measure 0.13×0.07 mm.

Echinostoma ilocanum (Garrison, 1908) (= *Fascioletta ilocana* Garrison) occurs in the intestine of man in the Philippines. It is a small form, measuring 4 to 6×0.75 to 1.35 mm. The eggs measure 0.088 to 0.111 $\times$ 0.053 to 0.074 mm.

In the genus **Hypoderæum** Dietz, 1909, the body is cylindrical, elongate and tapering behind. The ventral sucker is relatively large and situated near the anterior end. The portion of the body in front of it is flattened and curved ventrally, and is much thinner than the posterior portion. The cuticle is spiny. The "head-crown" is poorly developed, but bears a double row of spines, not interrupted dorsally. The œsophagus is very short. The cirrus-sac is elongate, reaching posteriorly as far as the hinder edge of the ventral sucker. The testes are elongate and situated one behind the other in the middle line. The adult worms usually live in the lower part of the intestine of birds.

Hypoderæum conoideum (Bloch, 1782) is found in the duck, goose and fowl, besides a number of wild ducks and geese. It may measure as much as 12×2 mm., and has an oral sucker measuring 0.28 mm. and a ventral sucker measuring 1 mm. in diameter. The "head-crown" contains forty-nine spines, of which the longest are only 0.04 mm. in length. The eggs measure 0.018×0.068 mm.

The intermediate hosts recorded for this species are *Limnæa peregra*, *L. stagnalis*, *L. limosa* and *Planorbis corneus*.

A species of "*Echinostoma*" was recorded by Müller in 1897 from the small intestine of the pigeon. It was only 0.6 mm. long. The oral sucker measured 0.14 mm., and the ventral sucker, which was at about the middle of the body, 0.24 mm. The cirrus-sac apparently extended

right round the ventral sucker on the right side, and the vitelline glands extended from the posterior limit of the testes as far as the anterior border of the ventral sucker. From the great length of the cirrus-sac it seems possible that this form belonged to *Hypoderæum*.

Echinoparyphium Dietz, 1909, consists of small forms with a slender body. The ventral sucker is at about the anterior quarter of the body. The "head-crown" has a double row of spines, uninterrupted dorsally, and the cuticle of the body is spiny. The cirrus-sac partly overlaps the ventral sucker. The testes are elliptical, one being placed immediately behind the other. The vitelline glands extend forward not quite as far as the ventral sucker. The adult worms live in the intestine of birds.

This genus is represented in domestic birds by **E. recurvatum** (v. Linstow, 1873), which occurs in the duck, fowl and several kinds of wild ducks. Its length is about 2·8 to 5 mm. and its width 0·5 to 0·85 mm. The oral sucker measures 0·12 to 0·13 mm. in diameter, and the ventral sucker 0·32 to 0·35 mm. The number of spines in the "head-crown" is forty-five, and these are of two sizes, arranged alternately. The eggs measure 0·088 to 0·1 × 0·056 to 0·06 mm. The intermediate hosts recorded for this species are *Planorbis planorbis*, *Limnæa limosa*, *L. palustris* and *Cyclas* sp.

In **Euparyphium** Dietz, 1909, the body is elongate, and the ventral sucker is large and situated close to the oral sucker. The entire ventral surface is spiny, but on the dorsal surface spines occur only in the anterior portion. The "head-crown" has a double row of spines, not interrupted dorsally. The cirrus-sac is of elongate oval shape, and extends posteriorly as far as the middle, or slightly beyond the middle, of the ventral sucker. The testes are typically much elongate, and may be curved or sinuous, with smooth outlines, and are placed in the middle line, one close behind the other. The ovary is round and usually median. The vitelline glands extend inwards behind the testes, leaving only a narrow median space unoccupied. Anteriorly they do not reach the ventral sucker. The uterus is short, with few coils. The eggs are relatively few. The adults occur in birds and mammals.

A few species which have been attributed to this genus, but do not appear to be very typical of it, occur in man or domestic animals. **E. malayanum** (Leiper, 1911) occurs in the small intestine of man in the Malay Peninsula. In this form the body is stout and rounded at both ends, and measures 8 to 12 × 3 to 3·3 mm. The ventral sucker is several times as large as the oral sucker, measuring 0·9 to 1·0 mm. in diameter. The diameter of the pharynx is 0·25 to 0·3 mm. The testes are deeply lobed. The vitelline glands meet across the body behind the testes.

The cirrus-sac extends behind the middle of the ventral sucker. The eggs measure 0.12 to 0.13×0.08 to 0.09 mm.

Euparyphium sufrartifex (Lane, 1915), which is known only from the original specimens (expelled by anthelmintic treatment from a girl in Assam, and in rather poor condition), has been regarded by some authorities as probably identical with *E. malayanum*. Lane, however, and more recently Faust (who has re-examined some of the type-specimens of *E. sufrartifex*), have pointed out that it differs from *E. malayanum* in the size and extent of the cirrus-sac. This organ extends backwards behind the posterior border of the ventral sucker. In *E. malayanum*, according to Lane, the anterior testis is the smaller, and the posterior testis is widely separated from the posterior end of the body. In *E. sufrartifex* the anterior testis is the larger, and the posterior testis nearly reaches the posterior end.

E. sufrartifex measures up to 9×2.5 mm. The diameter of the oral sucker is about 0.3 mm., that of the ventral sucker about 1 mm. The "head-crown" has thirty-nine (?) spines. The eggs measure 0.09×0.075 mm.

E. jassyense Léon and Ciurea, 1922, was obtained from a human being of Persian origin in Roumania, who was suffering from intermittent diarrhoea, and who recovered after anthelmintic treatment with thymol. The body of the worm was pinkish, measuring 5.44 to 7.6×1.05 to 1.38 mm. The cuticle was armed with rectangular spines, which were observed only on the lateral edges and extended nearly to the posterior end. The "head-crown" had twenty-seven spines, not interrupted dorsally. The oral sucker measured 0.22 mm. in diameter, the ventral sucker 0.73 mm. The cirrus-sac extended beyond the middle of the ventral sucker. The testes lay entirely or almost entirely in the anterior half of the body, one close behind the other, and were slightly lobed. The ovary lay to the right, in front of the anterior testis. The vitelline glands extended forward as far as the ovary, but not as far as the ventral sucker. The eggs were oval, measuring 0.132 to 0.154×0.079 to 0.085 mm.

Ciurea has obtained another form (**E. suinum** Ciurea, 1921) from two pigs which had been experimentally fed upon fishes (pike, tench and bream). These fishes are therefore probably intermediate hosts for the species. The adult worms recovered from the pigs measured 2.73 to 3.59×0.82 to 1.22 mm. The body was tongue-shaped, and the cuticle was covered with scales all over the ventral surface and on the anterior portion of the dorsal surface. The "head-crown" contained twenty-seven spines, and was uninterrupted dorsally. The oral and ventral suckers measured 0.3 and 0.5 mm. respectively, and the pharynx

0.18 mm., in diameter. The cirrus-sac almost reached the posterior edge of the ventral sucker. The testes were placed one behind the other in the middle of the body, and were slightly lobed. The ovary lay in front and to the right of the anterior testis. The eggs were lemon-shaped, measuring 0.117 to 0.127×0.078 to 0.088 mm.

In *Echinochasmus* Dietz, 1909, the body is short, widened behind the ventral sucker and rounded behind. The cuticle of the anterior region is spiny. The "head-crown" is well developed, and has a single row of twenty-four spines, which is interrupted in the mid-dorsal line. The cirrus-sac is small and lies almost entirely in front of the ventral sucker. The testes are large and transversely elongate, lying one behind the other midway between the ventral sucker and the posterior end. The ovary lies to the right of the median line, close in front of the anterior testis. The vitelline glands extend inwards almost to the middle line behind the testes, and forwards to a little in front of the posterior edge of the ventral sucker. The adults occur in the intestine of birds and mammals.

Echinochasmus perfoliatus (v. Rätz, 1908) is a parasite of the dog, cat and pig in Europe and Asia, and a variety (*japonicus* Tanabe) occurs in man in Japan. The animal measures about 2 to 4 mm. in length, and 0.4 to 1.0 mm. in width. The oral sucker has a diameter of 0.085 to 0.1 mm., and the ventral sucker is about twice as large. The eggs measure 0.1 to 0.11×0.065 to 0.074 mm. Cases of severe enteritis in the dog have been attributed to infection with this worm.

In Europe the metacercariæ occur, according to Ciurea, encysted in the scales, lateral line canal, etc., of various fresh-water fishes (*Abramis brama*, *Esox lucius*, *Aspius aspius*, *Idus idus*, *Blicca björkna*). Tanabe has also found fishes to be the intermediate hosts of the Japanese form.

In *Episthmium* Lühe, 1909, the body is elongate, and the "head-crown" has a single row of spines, which is interrupted dorsally. There are relatively sparsely distributed spines on the anterior region of the



FIG. 25.—*Echinochasmus perfoliatus*: VENTRAL VIEW. (AFTER V. RÄTZ.)

h., "head-crown"; or., ovary; sem., seminal vesicle; t., testis; v.s., ventral sucker.

body. The cirrus-sac is small, and lies entirely or almost entirely in front of the ventral sucker. The posterior testis is longer than the anterior, and both lie close together in the middle line and in the posterior half of the body. The ovary is rounded, and lies medially in front of the testes. The vitellaria are well developed, extending forward as far as the pharynx, and confluent in the middle line both in front and behind. The uterus is relatively short and the eggs few. The adults occur in the bursa Fabricii of birds.

E. oscari Travassos, 1923, is recorded from the bursa Fabricii of the fowl in Brazil. It is a form measuring 6 mm. in length and 2 mm. in width, with a reduced "head-crown" and poorly-developed spines. The oral sucker is 0.29 mm. in diameter, the ventral sucker 0.34 mm. and the pharynx 0.17 mm. The cirrus-sac is 0.6 mm. long. The eggs measure 0.127×0.056 mm.

PSILOSTOMIDÆ.

The **Psilostomidæ** are small or medium-sized flukes with a muscular and usually only slightly flattened body. The cuticle may or may not be spiny. The suckers are large. A pharynx is present. The œsophagus, when present, is short. The intestinal branches are simple and reach the posterior end of the body. The genital pore is somewhat in front of the ventral sucker and to the left of the middle line. The cirrus-sac is large but not very muscular. The testes are large, median, and placed one close behind the other in the hinder part of the body. The ovary is rounded or oval, and lies between the ventral sucker and the anterior testis. The vitelline glands are well developed, lateral, partly overlapping the intestinal cæca, and confluent behind the testes. The uterus is short, its coils lying between the anterior testis and the ventral sucker. The eggs are large and not very numerous.

The members of this family (which contains about seven genera) are mainly found in the intestine of aquatic birds, but one species, **Testi-frondosa cristata** Bhalerao, 1924, which occurs in a mammal, has been attributed to the group. In this form, which occurs in the intestine of pigs (*Sus cristatus*) in Burma, the body is covered with scales, and measures 6 to 8 mm. in length and 2.5 to 3.5 mm. in width. The oral sucker has a diameter of 0.22 mm. The ventral sucker is larger, measuring 1.02×0.82 mm., and has a sac-like posterior prolongation. It is placed at about the anterior fifth of the body. There is a small globular pharynx, 0.18 mm. in diameter, and a short œsophagus. The genital pore is near the intestinal bifurcation. The cirrus-sac is much elongated, extending posteriorly behind the ventral sucker. The testes are branched and lie one behind the other in the posterior half of the body. The eggs measure 0.11 to 0.13×0.07 to 0.08 mm.

In *Psilochasmus* Lühe, 1909, the body is slender and lancet-shaped and terminates posteriorly in a retractile point. The anterior end is conical. The cuticle is without spines. The ventral sucker is very deep and prominent, and is situated at the anterior third of the body. An œsophagus is present, and the intestinal bifurcation is close in front of the ventral sucker. The testes are large, elongate and deeply lobate laterally. The ovary is rounded, and is separated from the testes by the shell-gland. The vitellaria consist of numerous follicles, and extend from the posterior limit of the ventral sucker almost to the posterior end.

P. lecithosus Otte, 1926, is recorded from the intestine of the duck in Germany. It is a species measuring 4 to 11 mm. in length and 2 to 2.5 mm. in width. The oral sucker is about 0.26 mm. in diameter, the ventral sucker about 1.2 mm. and the pharynx about 0.2 mm. The testes are of elongate oval shape, situated one close behind the other and flattened where they are in contact. The elongate excretory bladder opens on a small, invaginable papilla. The eggs measure 0.09 to 0.1 $\times$ 0.055 to 0.06 mm.

HARMOSTOMIDÆ.

The *Harmostomidæ* are more or less elongate flukes of variable form. The cuticle is smooth or only slightly spiny. A pharynx and a very short œsophagus are present. The intestinal cæca extend to the posterior end of the body. The excretory bladder is Y-shaped, with a short stem and long branches. The ovary lies between the testes. The genital pore is near the posterior end (median or somewhat lateral), or even terminal. The adult worms are parasitic in the intestine of vertebrates. The family contains twelve genera.

The genus *Harmostomum* Braun, 1899, consists of forms with a somewhat elongate body, with a smooth cuticle or with small spines anteriorly. The genital pore is in the neighbourhood of the level of the anterior border of the anterior testis. The adults occur in the intestine of mammals and birds. The cercariæ of some species are known to occur in snails of the genus *Helix*.

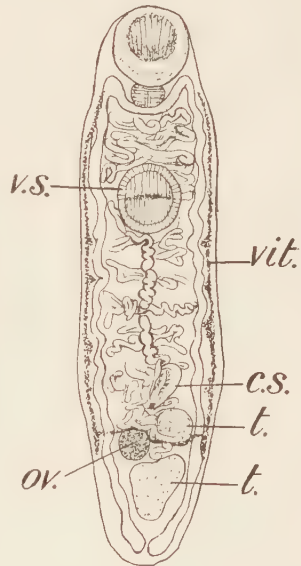


FIG. 26.—*Harmostomum commutatum*: VENTRAL VIEW. (AFTER WAGENER, MODIFIED.)

c.s., cirrus-sac; ov., ovary; t., t., testes; vit., vitellaria; v.s., ventral sucker.

Harmostomum commutatum (Diesing, 1858) occurs in the cæca of the fowl, turkey, guinea-fowl and pigeon in Southern Europe, North Africa and Indo-China. It may apparently cause an inflammatory condition of the cæca. The body of this worm is somewhat tongue-shaped, and measures 3.5 to 7.5 mm. in length and 1 to 2 mm. in width. The oral sucker measures 0.23 to 0.69 mm. in diameter, and the ventral sucker 0.39 to 0.75 mm. The eggs measure 0.029 to 0.032×0.018 mm.

A species occurring in the small intestine of the domestic pigeon in Brazil has been described by Travassos (1927) under the name of **H. mazzantii**. This is possibly identical with the "*Distoma columbæ*" described from the pigeon in Europe by Mazzanti in 1889. The Brazilian form measures 2.2 to 6.2 mm. in length and 0.4 to 1.1 mm. in width. The ventral sucker is smaller than the oral sucker, measuring 0.15 to 0.3 mm. in diameter. The oral sucker measures 0.23 to 0.4 mm. The eggs measure 0.035 to 0.045×0.027 to 0.03 mm.

SCHISTOSOMATIDÆ.

The **Schistosomatidæ**, or "blood-flukes," are remarkable in many respects, but their most striking peculiarity is the fact that the sexes are separate and usually of quite dissimilar appearance. The male is stouter than the female, and the posterior portion of its body, though flattened, usually has its edges folded inwards in such a way as to form a deep groove (the gynæcophoral groove or canal) in which the female is carried. The female, on the contrary, is usually slender and cylindrical in shape. Suckers may be present or absent in both sexes. The ventral sucker, when present, lies in front of the genital pore. A pharynx is absent, and the two intestinal branches, though present, unite posteriorly, after a longer or shorter course, to form a single cæcum. The male has four or more testes, and the female a single, compact ovary, lying in front of the posterior union of the intestinal branches.

The family contains some seven genera, the members of which inhabit, as adults, the blood-vessels of mammals and birds. The larval stages occur in snails, the miracidium developing into a sporocyst in which cercariæ are formed without the intervention of a redia stage. The cercariæ are fork-tailed (furcocercous), and without a pharynx or eye-spots, but provided with an anterior piercing stylet and with several pairs of "salivary" glands connected with the mouth.

In the genus **Schistosoma** Weinland, 1858 (= *Bilharzia* Cobbold, 1859), the ventral sucker is larger than the oral sucker, and rather prominent. The intestine divides into two branches at about the level of the ventral sucker, and these unite again into a single cæcum posteriorly. The

anterior portion of the body, in the male, is short, narrow and cylindrical, the portion behind the ventral sucker being much broader and forming the gynæcophoral canal. The genital pore lies in the mid-ventral line immediately behind the ventral sucker. The testes form a group lying a little behind the genital pore. The body of the female is cylindrical and much more slender than that of the male. The ovary is elongate-oval in shape, and is usually situated behind the middle of the body. The vitelline glands are arranged in a series of groups on either side of the single intestinal cæcum, in the posterior region. The uterus is a simple, straight tube, and the eggs are comparatively large and produced in relatively small numbers at a time. They are thin-shelled, and occur in two forms in different species, one oval with a terminal or lateral spine, the other elongate and spindle-shaped, with one end produced into a spine.

The adults occur in mammals, inhabiting chiefly the portal and mesenteric veins. The larval stages are parasitic in fresh-water snails, the cercariæ ultimately escaping into water and having the power of penetrating the skin or mucous membranes of suitable definitive hosts with which they may come in contact.

Of this genus four (possibly five) species occur in man, while four more have been recorded from domestic animals.

Schistosoma hæmatobium (von Siebold, 1852), the form originally discovered by Bilharz in Egypt, is an important human parasite of rather wide distribution. Besides Egypt, where it is particularly prevalent, it occurs in other parts of Northern Africa, as well as in the east, south and west of that continent, and also in Arabia, Cyprus, Greece, certain localities in Portugal, and Australia.

The male measures 10 to 15 mm. in length, and about 1 mm. in

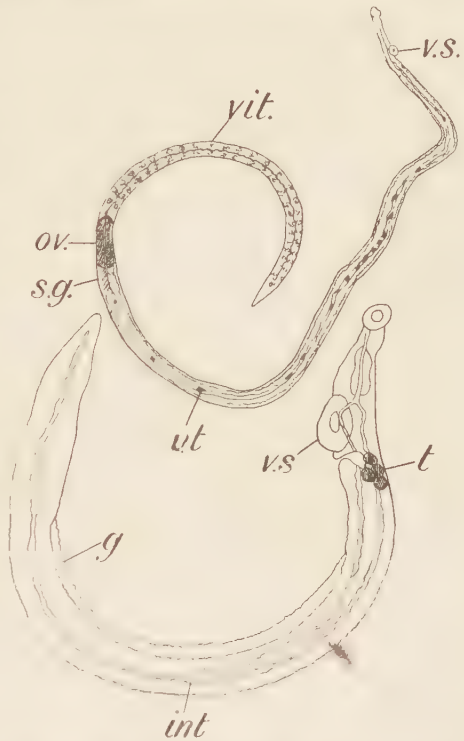


FIG. 27. *Schistosoma hæmatobium*: FEMALE ABOVE, MALE BELOW. (AFTER MANSON-BAHR AND FAIRLEY.)

g., gynæcophoral canal; ov., ovary; s.g., shell gland; t., testes; ut., uterus; vit., vitellaria; v.s., ventral sucker.

thickness. Its cuticle is finely tuberculated. The testes are relatively large and four or five in number. The female measures 15 to 20 mm. in length and only 0.1 to 0.25 mm. in diameter. The intestinal branches, in the female, reunite in the posterior third of the body, within which the ovary is also situated. The vitelline glands occupy the posterior quarter. The eggs are relatively numerous, and are of an elongate oval shape, with a terminal spine. They measure 0.15 to 0.16×0.04 to 0.06 mm.

The adults inhabit the mesenteric, splenic, vesical and portal veins, and sometimes the inferior vena cava. So far as is known, man is the only natural definitive host of this species. The eggs block and perforate the capillaries in the wall of the bladder, and escape to the exterior with the urine, causing in the process the "endemic hæmaturia" which is so well-known a disease in Egypt and elsewhere. The intermediate hosts are, in Egypt, the fresh-water snails *Bullinus contortus* and *B. dybowskii* (= *Physa alexandrina*); in South Africa, *Bullinus* [*Physopsis*] *africanus* and *Limnæa natalensis*; in the Sudan, probably *Isidora innesi*; in the Gold Coast and Nyasaland, *Physopsis globosa*; at Sierra Leone, a species of *Physopsis*, near *P. globosa*; in Portugal, probably *Planorbis corneus*, var. *metidjensis*. The cercaria of *S. hæmatobium* has three pairs of 'salivary' or "mucin" glands, which exhibit an acidophil staining reaction.

Schistosoma mansoni Sambon, 1907, occurs in man in Egypt, South Africa, the Congo region, Nyasaland, Madagascar, the Southern United States, South America and the West Indies. The form of schistosomiasis caused by this species affects the colon, rather than the bladder as in the case of *S. hæmatobium*. The eggs escape to the exterior usually with the fæces, and only exceptionally with the urine.

The male measures about 10 to 12 mm. in length and 0.45 to 1.2 mm. in diameter; the female up to 16 mm. and 0.16 to 0.17 mm. respectively. The cuticle of the male is relatively coarsely tuberculated. The testes are relatively small and eight in number. In the female the ovary and the point of union of the branches of the alimentary canal are within the anterior half of the body, while the vitelline glands occupy the posterior half. The eggs (of which there is usually only one in the uterus at a time) have a stout lateral spine, and measure 0.112 to 0.162×0.06 to 0.07 mm.

The intermediate hosts of *S. mansoni* are: in Egypt, *Planorbis boissyi*; in South Africa, *Planorbis pfeifferi*, *Physopsis africana* and *Isidora tropica*; in South America, *Planorbis olivaceus*, *P. guadeloupensis* and *P. centimetralis*; in the West Indies, probably *Planorbis antiguensis*; in Nyasaland, a species of *Planorbis*, near *P. sudanicus*. The cercaria may be distinguished by the possession of six pairs of "salivary" glands, of which two are large and four small.

In the Far East (Japan, Formosa, China and the Philippines) the place of the two previously described human Schistosomes is taken by a third species, *S. japonicum* Katsurada, 1904 (= *S. cattoi* Blanchard, 1905). This form occurs in the portal vein and arteries, and is found, as well as in man, in various domestic animals—cattle (*Bos sinicus*), goat, horse, pig, cat and dog. The male is 9 to 12 mm. long and 0.5 to 1 mm. in thickness, the female 12 to 15 mm. and 0.3 to 0.4 mm. respectively. In both sexes the suckers are spiny, while in the male the spines extend over the ventral surface of the body, the rest of the cuticle being smooth. The male has from six to eight oval testes. In the female the ovary is situated in the middle of the body, and the vitelline glands in the posterior half. The eggs are of rounded oval shape, and provided laterally with a small spine, a papilla, or a mere thickening. They measure $0.083 \times 0.098 \times 0.062$ to 0.074 mm. The eggs escape from the blood-vessels into the liver and the wall of the colon, and reach the exterior with the fæces.

The intermediate hosts of *S. japonicum* are: in Japan, *Katayama nosophora* (= *Blanfordia japonica*); in China, *Katayama fausti* and *Oncomelania hupensis*; in Formosa, *Katayama* [*Blanfordia*] *formosana*. The cercaria possesses five pairs of small, granular "salivary" glands.

Schistosoma bovis (= *S. crassum*) Sonsino, 1876, occurs in the abdominal veins of the ox and sheep in Egypt, Sicily, Sardinia, the South of France, South and East Africa, India, the Malay States and Indo-China. It causes lesions similar to those of *S. mansoni*, including sometimes cirrhosis of the liver. The male measures 9 to 20 mm. in length and 1 to 1.2 mm. in thickness, and its cuticle, except on the anterior portion, is covered dorsally with small spine-bearing tubercles. The ventral sucker is also lined with spines. The intestinal branches reunite at about the posterior fourth of the body. There may be several junctions between them, and occasionally there are two posterior cæca. The testes vary in number from three to six, the usual number being four.

The female is 12 to 20 mm. long. The uterus sometimes contains as many as thirty-three eggs, but often as few as four or five. These measure $0.16 \times 0.18 \times 0.045$ to 0.06 mm., and are spindle-shaped, with a terminal spine at one end. They reach the exterior with the fæces, and possibly also with the urine, of the host.

In South Africa the intermediate host of *S. bovis* is said to be probably *Physopsis africana*. The cercaria has four pairs of "salivary" glands, of which two are acidophil and two basophil when stained.

S. bomfordi Montgomery, 1906, occurs in the mesenteric veins of the zebu in India, and has also been recorded from the ox in France. The male is 6 to 9 mm. long and 0.4 to 1 mm. thick, the female 3 to

7.31 mm. and 0.1 to 0.17 mm. respectively. The cuticle of the male is studded with tubercles, each bearing a variable number of delicate spines.

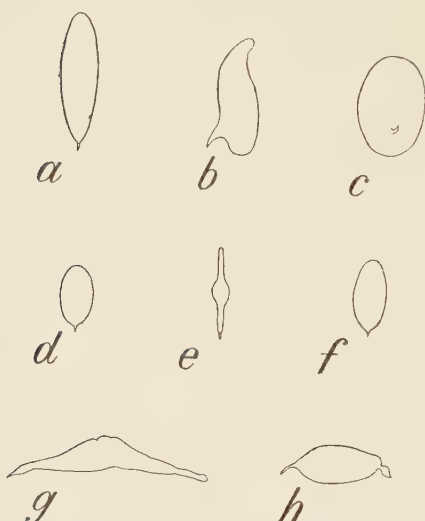


FIG. 28.—OUTLINES OF THE EGGS OF VARIOUS SPECIES OF *Schistosoma*. (AFTER SKRJABIN.)

a, *S. hæmatobium*; b, *S. mansoni*; c, *S. japonicum*; d, *S. indicum*; e, *S. bovis*; f, *S. bomfordi*; g, *S. spindalis*; h, *S. turkestanicum*.

and about 0.2 mm. in thickness. There are small spines in the oral sucker and on the tail. The paired intestinal branches are longer than the posterior cæcum. The ovary is in the middle of the body. The eggs are greatly elongate and flattened on one side, and have a straight, slender spine at one end. They measure 0.248 to 0.4 × 0.044 to 0.072 mm.

The intermediate hosts are *Planorbis exustus* and *Limnæa acuminata*. The cercaria has five pairs of "salivary" glands, of which two are acidophil and three basophil in staining reaction.

S. indicum Montgomery, 1906, occurs in the portal and mesenteric veins of the donkey, horse, sheep and camel in India. This species is very variable in size, and, according to Montgomery's measurements, seems to attain a much greater size in the donkey than in the horse. The male is 8.35 to 19 mm. long and 0.35 to 0.5 mm. thick. Its cuticle is covered with tubercles, which are more numerous on the dorsal surface

There are about sixty testes, arranged in a longitudinal series between the intestinal branches. The female closely resembles that of *S. hæmatobium*. The posterior intestinal cæcum is nearly three times as long as the paired branches. The eggs are small and oval, with a terminal spine. They measure 0.1 to 0.136 × 0.044 to 0.06 mm.

S. spindalis Montgomery, 1906, is a parasite of the zebu and ox in India and Sumatra.* Like the previous species, it occurs in the mesenteric veins. The male measures 8.24 to 9.58 mm. in length and 0.527 mm. in thickness. Its cuticle is tuberculated, while the suckers and the edges of the gynæcophoral groove are spiny. There are six or seven testes. The female measures up to 14.11 mm. in length

* A form observed twice in man in South Africa, in persons who had been closely associated with cattle or goats, has been named *S. spindalis* var. *africana* Porter, 1926. The eggs found in the urine measured only 0.163 to 0.258 × 0.0464 to 0.07 mm. *Planorbis pfeifferi* was experimentally infected with the miracidia, and a male worm recovered from an experimental rat.

than elsewhere. Each tubercle carries on its summit six to twelve fine spines. There are from five to nine testes. The female measures 10 to 28 mm. in length and 0.12 to 0.263 mm. in thickness. Its cuticle is without tubercles or spines except inside the suckers and on the posterior extremity. The ovary is in the middle of the body. The uterus occupies almost half the distance between the ventral sucker and the posterior end, and contains numerous eggs arranged in a single row. The eggs are oval, with a terminal spine, and measure 0.09 to 0.14×0.042 to 0.072 mm. They reach the exterior with the host's fæces.

S. turkestanicum Skrjabin, 1913, is a small form found in the portal system of cattle in Russian Turkestan. The male measures 4.2 to 8 mm. in length and 0.34 to 0.476 mm. in thickness, the female 3.4 to 5.5 mm. and 0.102 mm. respectively. The cuticle is without tubercles. The testes of the male are very numerous (seventy-eight to eighty), and extend for a distance of about 3 mm. In the female, the posterior cæcum of the intestine is about three times as long as the divided portion. The ovary is swollen behind and tapering in front, and is spirally twisted about its longitudinal axis. The uterus contains a single egg at a time. The eggs are oval, with a slender spine at one end and an irregularly shaped process at the other. They measure 0.0725 to 0.074×0.0222 to 0.0261 mm.

Schistosoma incognitum Chandler, 1926, is a supposed species based on eggs, unlike those of any of the forms already mentioned, which were found on two occasions in human fæces in Bengal. These eggs were oval, but slightly flattened on one side, and carried a spine which was nearly terminal, but inclined slightly towards the flattened side. They measured 0.095 to 0.1×0.0415 to 0.05 mm.

The genus **Bilharziella** Looss, 1899, is closely related to the Schistosomes. The species **B. polonica** (Kowalewski, 1895), which occurs in the blood-vessels of certain wild ducks in Central Europe, has also been recorded from the domestic duck.* In this form the body is flattened in both sexes, and has a lancet-shaped expansion in its posterior half. The male measures about 4 mm. in length and 0.52 mm. in width, while the female is only of about half these dimensions. The intestine divides a little in front of the ventral sucker into two branches, which reunite, as in *Schistosoma*, at about the middle of the body to form a long posterior cæcum. In the male the genital pore is displaced towards the left side, and situated some distance behind the ventral sucker, near the level of the union of the intestinal branches. The testes are very numerous, and arranged in a single row on each side of the posterior intestinal cæcum, extending throughout its length. In the female the genital pore is

* Oiso has recently described a smaller species, *B. yokogawai*, from the duck in Formosa. Its intermediate host is *Limnæa radix*.

median, and close behind the ventral sucker. The uterus is short, and contains but a single, relatively very large, egg at a time. The eggs are much elongated at one end, and have a short terminal spine at the other. They measure about 0.4×0.1 mm.

STRIGEIDÆ.

In the family **Strigeidæ** (or **Holostomidæ**) the body is usually more or less distinctly divided by a constriction into two portions, of which the anterior carries the suckers and the posterior contains most of the genital organs. The anterior region is generally flattened, with ventrally incurved edges, or cup-shaped. The posterior portion is usually cylindrical or oval. The ventral sucker is generally poorly developed, but behind it there is developed a special "adhesive organ" of varying form. A pharynx and an œsophagus are present, and the intestinal cæca are simple and usually extend to the posterior end of the body. The genital pore is at or near the posterior end. A cirrus and cirrus-sac may be present or absent. The uterus is short and the eggs relatively few and large.

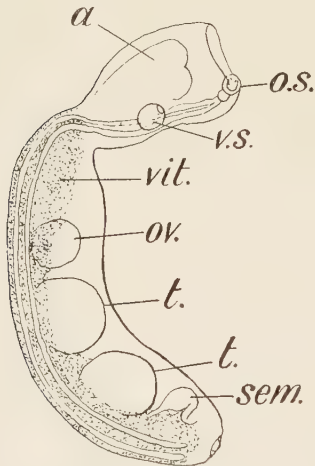


FIG. 29.—*Strigea gracilis*: LATERAL VIEW. (AFTER BRANDES.)

a., adhesive organ; o.s., oral sucker; ov., ovary; sem., seminal vesicle; t., t., testes; vit., vitellaria; v.s., ventral sucker.

The adult worms are classified in about a dozen genera, and are chiefly parasites of the alimentary canal of birds. The cercariæ are fork-tailed and possess a pharynx, and develop in slender sporocysts in snails. The metacercariæ possess some of the characters of the adults (special clinging organs), and occur in snails, leeches and various vertebrates.

In *Strigea* Abildgaard, 1790, the anterior and posterior regions of the body are sharply separated. The lateral margins of the anterior portion are fused ventrally so as to form a cup-shaped structure which encloses the ventral sucker and the "adhesive organ." There is no cirrus or cirrus-sac.

Strigea gracilis (Rudolphi, 1819), which occurs in several kinds of wild duck in Europe, has also been recorded from the domestic duck. It is a form about 2.5 mm. long, in which the posterior portion of the body is of an elongate oval shape, and longer and narrower than the anterior portion. The oral sucker is 0.13 mm., and the ventral sucker 0.2 mm., in diameter. The eggs measure 0.11×0.067 mm.

S. tarda (Steenstrup, 1842) occurs in the intestine of the duck, goose and swan, besides a number of wild ducks and other birds. This form is from 1.2 mm. to perhaps as much as 3 mm. in length, and has a short, goblet-shaped anterior portion, not much wider than the oval posterior portion. The ventral sucker is larger than the oral sucker. The genital opening is somewhat on the dorsal side of the rounded posterior extremity. The larval form of this species is apparently "*Tetracotyle typica*," which occurs in the tissues of fresh-water snails of the genera *Limnæa*, *Planorbis* and *Vivipara*.

The genus **Parastrigea** Szidat, 1928, resembles *Strigea* in most respects, but differs from it in the form of the anterior, cup-shaped portion of the body, which has two large lateral expansions, while its aperture is very narrow. **P. robusta** Szidat, 1928, is a species found in the intestine of the duck in Germany.

In **Prohemistomum** Odhner, 1913, the body is short and broad, more or less oval, and not distinctly divided into anterior and posterior portions. It is flattened in front of the "adhesive organ," which takes the form of a knob-like process. Behind this organ the lateral margins are united ventrally. The cuticle is armed with spines or scales. A cirrus and cirrus-sac are present, the latter being elongate and situated ventrally to the testes. The ovary is small and lies ventrally to the anterior testis. The vitelline glands consist of large, distinct acini, and sometimes extend into the "adhesive organ." The type-species of this genus is a parasite of the kite, but two other species occur in the dog and cat.

Prohemistomum appendiculatum Ciurea, 1916, measures 0.9 to 1.75 mm. in length and 0.4 to 0.6 mm. in width. The posterior part of the body tapers to form a cylindrical appendage. The "adhesive organ" is relatively small. The oral sucker is 0.055 to 0.09 mm. in diameter, and the ventral sucker measures 0.05 to 0.085 × 0.065 to 0.095 mm. There are only four or five eggs in the uterus at a time, and these measure 0.1 to 0.117 × 0.063 to 0.068 mm. This worm was obtained experimentally in the intestine

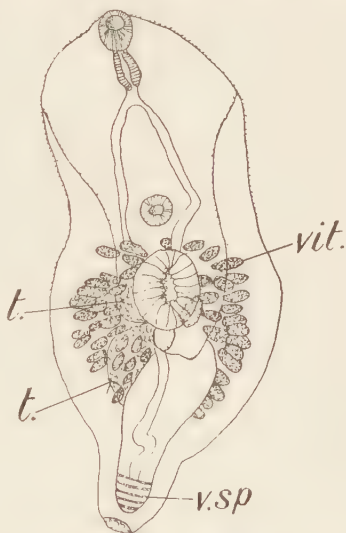


FIG. 30. — *Prohemistomum appendiculatum*: VENTRAL VIEW. (AFTER TUBANGUI.)

t., t., testes; vit., vitellaria;
v. sp., vaginal sphincter.

of dogs and cats by Ciurea in Roumania, after feeding them with the intermediate hosts (fishes of the genera *Tinca*, *Aspius*, *Carassius*, *Blicca*, etc.).

Prohemistomum industrium Tubanguï, 1922, was found occurring naturally in the intestine of the dog in China. The body in this species is somewhat pyriform, and measures 1.5 to 1.9×1 to 1.2 mm. The "adhesive organ" is highly developed and dome-shaped. The oral sucker measures 0.1 to 0.13×0.13 to 0.14 mm., and the ventral sucker 0.1 to 0.11 mm. in diameter. The dimensions of the cirrus-sac are 0.7 to 0.9×0.08 to 0.13 mm. The eggs measure 0.13 to 0.146×0.089 to 0.097 mm.

In the genus **Alaria** Schrank, 1788, the anterior region of the body is flattened and more or less expanded laterally. The posterior region is cylindrical or flattened. At the sides of the oral sucker there is usually a pair of accessory sucker-like organs, ear-like projections or tentacle-like appendages. The "adhesive organ" consists of two long folds. There is no cirrus or cirrus-sac. The vitelline glands are mainly in the anterior region of the body, and the uterus extends into the "adhesive organ."

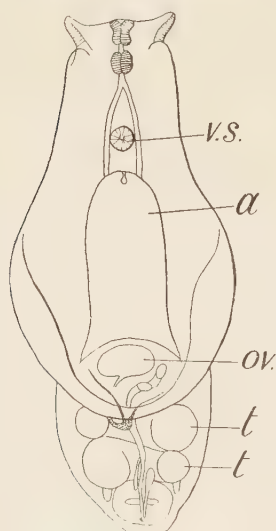


FIG. 31.—*Alaria alata*:
VENTRAL VIEW. (AFTER
BRANDES, MODIFIED.)

a., adhesive organ; ov., ovary;
t., t., testes; v.s., ventral
sucker.

Alaria alata (Goeze, 1782) occurs in the stomach and intestine of the dog, cat, wolf and fox in Europe. It is 3 to 6 mm. long, with the anterior portion much longer than the posterior. There is a pair of prominent crescentic projections at the sides of the oral sucker. The oral sucker is somewhat larger than the ventral. Two closely related species have been described from carnivorous mammals in North America—viz., **A. americana** and **A. michiganensis** Hall and Wigdor, 1918.

The former is 3 to 5 mm. long, and has well-developed crescentic projections anteriorly, like those of *A. alata*. It has been found in the dog, cat and fox. The second species is smaller (1.8 to 1.91 mm. long), and is without the crescentic projections. It has been found in the dog at Detroit, Michigan.

In **Pharyngostomum** Ciurea, 1922, the body is stout, and is not very distinctly separated into anterior and posterior regions. The animal is very similar in structure to *Alaria*, but the adhesive organ is large and

somewhat heart-shaped. The testes are deeply lobate and situated nearly opposite to each other.

P. cordatum (Diesing, 1850) is a parasite of the intestine of the wild cat in Europe, but does not appear to be of general occurrence in the domestic cat. Recently, however, it has been found by Faust occurring naturally in a domestic cat in China, and he has shown that its immature form occurs in certain fresh-water fishes (*Rhodeus sinensis*, *Eleotris potamophilia*). The adult worm is 2.6 to 3.8 mm. long and 1.58 to 1.98 mm. broad. The oral sucker measures about 0.2 mm., the ventral sucker about 0.06 mm. in diameter, and both suckers are concealed by the adhesive organ. There is a powerful pharynx, measuring 0.22 to 0.24 mm. in diameter.

PARAMPHISTOMIDÆ.

The group **Paramphistomida** or **Paramphistomoidea** was divided, in the classification proposed by Stiles and Goldberger in 1910, into a number of "superfamilies," families and subfamilies. This classification is not accepted by Poche, who regards the whole group as consisting of a single family, **Paramphistomidæ**. These are usually thick, fleshy forms in which the body is commonly more or less circular in transverse section, though there are exceptions. Their most characteristic feature is the position of the ventral sucker, which is placed at or near the posterior end of the body, and is often very highly developed. It is convenient, in this group, to speak of it as the posterior sucker. The cuticle is without spines. The genital pore is situated in the middle line, in front of the middle of the body. The testes are usually paired, and the ovary is usually behind them. The vitelline glands are usually very well developed. A pharynx is absent, but an œsophagus is present. The intestinal cæca are simple. The excretory pore is dorsally situated, near the posterior end of the body.

The adult worms occur in the alimentary canal or liver of vertebrates, and the intermediate hosts, so far as is known, are molluscs. The life-history is similar to that of the Fasciolidæ.

Stiles and Goldberger recognized a large number of species within this group, occurring largely in domestic ruminants. Maplestone, however, who has made a recent survey of these forms, has shown that there is a very large amount of variation within the species, and that many of the characters which had been considered specific can only be regarded as individual variations or as the results of different methods of preservation and different states of contraction in preserved specimens. Accordingly, the number of species occurring in domestic hosts is probably much smaller than had been supposed.

In *Paramphistomum* Fischöeder, 1901, the typical genus of the family, the body is pinkish white when fresh, and is more or less conical in shape, convex dorsally and slightly concave ventrally, rather attenuate in front and broad and blunt behind. The intestinal cæca extend posteriorly behind the testes. A cirrus-sac is absent. The testes are usually somewhat lobate.

Paramphistomum cervi (Schrank, 1790) appears to be chiefly an African form, but has a wide distribution. It occurs in the stomach (rumen) of cattle, zebu, Asiatic buffalo, sheep, goat, deer and antelopes. In size and shape the species is extremely variable, especially when preserved. In general its length is about 5 to 12 mm. Small papillæ are sometimes observable on the cuticle near the mouth. The genital pore is situated at about the anterior third of the body. The intestinal cæca terminate dorsally to the posterior sucker. The testes are somewhat lobate, and one is placed directly behind the other. The vitelline glands extend along the sides of the body, in coarse groups of follicles placed close together, from the level of the pharynx to the posterior border of the posterior sucker, and also spread on to the dorsal and ventral surfaces. The eggs measure 0.145 to 0.156 × 0.075 to 0.082 mm.

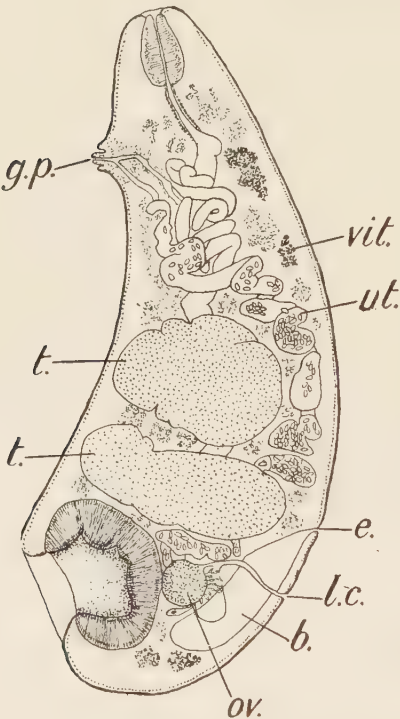


FIG. 32.—*Paramphistomum cervi*: RIGHT HALF OF A BISECTED SPECIMEN. (AFTER FISCHÖEDER.)

b., excretory bladder; e., excretory pore; g.p., genital pore; l.c., Laurer's canal; ov., ovary; t., t., testes; ut., uterus; vit., vitellaria.

P. anisocotylea Faust, 1920, a form found in the buffalo and ox in the Philippines, is apparently very closely related to *P. cervi*, but differs from it in the fact that its testes are rounded and not lobate.

P. gotoi Fukui, 1922, and *P. ichikawai* Fukui, 1922, both from the stomach of the ox in Japan (the latter also occurring in Formosa and Manchuria), are also very similar to *P. cervi*. In *P. gotoi* the body is

The intermediate hosts of this species in Egypt, according to Looss, are the pulmonate molluscs *Bullinus dybowski* and *B. forskali*.

covered with papillæ, except on the posterior two-thirds of the dorsal surface, about half of the sides and a portion of the ventral surface in front of the posterior sucker. The oral sucker is elongate, measuring about a sixth of the length of the body. Its inner surface, for the anterior two-fifths, is covered with papillæ which have flattened, denticulate ends. The lumen of the sucker is narrower in the posterior three-fifths. The chief characters said to distinguish *P. ichikawai* from *P. cervi* are the fact that the genital papilla is well developed and protrusible, and more like that of *P. explanatum*, and that the vitellaria are composed of small follicles, unlike those of *P. cervi*.

Paramphistomum explanatum (Creplin, 1847) externally resembles *P. cervi*, but is slightly flattened and, when fully grown, is easily recognized by the fact that the testes are placed diagonally, overlapping each other both laterally and antero-posteriorly. The length of the worm varies from 3 to 13 mm. This species occurs in the gall-bladder and ducts of the ox, buffalo and various antelopes, in Africa, Cochin-China and Australia.

P. ijimai Fukui, 1922, of which the original description is not available to the writer, is recorded from the ox in Japan, and, according to an abstract by Morishita, appears to be very closely related to *P. explanatum*.

Paramphistomum orthocœlium Fischöder, 1901, was originally recorded from the stomach of a buffalo that had died at Berlin. It has since been recorded from the ox and zebu, and by Maplestone from the sheep in China. In this form the straight intestinal cæca end somewhat in front of the posterior sucker, the testes are placed one behind the other, and the vitelline glands are arranged in large groups of follicles, usually in a single row laterally or ventrally to each intestinal cæcum, except near the posterior end, where they are grouped together. The eggs measure 0.105 to 0.115×0.06 to 0.065 mm.

Cotylophoron Stiles and Goldberger, 1910, resembles *Paramphistomum* in general appearance, but differs from that genus in the possession of a distinct *genital sucker* into which the genital ducts open.

Cotylophoron cotylophorum (Fischöder, 1901) (of which *C. indicum* Stiles and Goldberger is regarded as a synonym by Maplestone), occurs

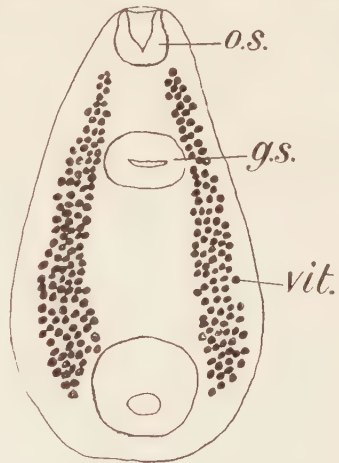


FIG. 33.—*Cotylophoron cotylophorum*: VENTRAL VIEW.
(AFTER FISCHÖDER.)

g.s., genital sucker; *o.s.*, oral sucker;
vit., vitellaria.

in the rumen of the ox, zebu, buffalo, sheep and antelopes in Africa and India. The worm measures 4 to 8 mm. in length.

In **Pseudodiscus** Sonsino, 1895 (—*Watsonius* Stiles and Goldberger, 1910), the body is oval or pyriform, convex dorsally, rounded behind and less blunt in front. The posterior sucker is subterminal, and has prominent margins. There is no genital sucker, and a cirrus-sac is absent. The oral sucker has a constriction in its middle and gives off posteriorly two globular pouches. The intestinal cæca extend behind the testes, and the ovary is also situated behind them.

Pseudodiscus collinsii (Cobbold, 1875) occurs in the colon of horses and mules in India. It is of a brick-red colour when fresh, and measures 4.5 to 9 × 1.4 to 5.7 mm. The diameter of the posterior sucker is 0.57 to 1.8 mm. A second form, *P. stanleyii*, was described by Cobbold from the horse in India, but the supposed differences do not, according to Maplestone, warrant the erection of two distinct species.

Pseudodiscus watsoni (Conyngham, 1904) occurs in the duodenum and small intestine of man and monkeys, in East and West Africa, and possibly in Japan. It measures 8 to 10 mm. in length and 4 to 5 mm. in width, and is reddish-yellow when fresh. The oral and posterior suckers both measure somewhat over 1 mm. in diameter. The eggs measure 0.12 to 0.13 × 0.075 to 0.08 mm. The genus *Watsonius* was proposed by Stiles and Goldberger for the reception of this form, as distinct from *Pseudodiscus*, but Maplestone believes that no reliance can be placed upon the characters in which it is said to differ from that genus.

Species attributed to *Pseudodiscus* and *Watsonius* also occur in the Indian elephant.

The remarkable genus **Balanorchis** Fiscoeder, 1901, possesses characters which suggest relationship both to *Cotylophoron* and to *Pseudodiscus*. The oral sucker gives off two well-developed pouches. The mouth is surrounded by a number of spiny papilliform processes. The protrusible cirrus-sac is surrounded by a genital sucker, on the hinder edge of which is the separate opening of the uterus. The intestinal cæca reach the posterior sucker. The testes are non-lobate, and are placed side by side close in front of the posterior sucker. The ovary lies dorsally in front of one of them. The vitelline glands are arranged in distinct spherical groups in a single S-shaped row on each side of the body. The excretory bladder lies dorsally and between the testes.

B. anastrophus Fiscoeder, 1901, was originally described from the stomach of deer from Brazil, but according to Travassos the form described under the name of *Verodunia tricornata* by Lahille and Joan in 1917, from the stomach of the ox in the Argentine, is identical with

it. According to Fiscoeder's description, the worm measures 3 to 4 mm. in length, and the mouth is surrounded by twelve to fifteen papilliform processes. The dimensions of the worms described by Lahille and Joan are larger (6 to 7×1.2 mm., with a posterior sucker 0.62 mm. in diameter), and the mouth is said to be surrounded by three rings of fourteen "tentacles." The vitelline glands, according to Fiscoeder, are in fourteen to eighteen groups on each side; according to Lahille and Joan, in twelve to fifteen groups. The eggs measure, according to Fiscoeder, 0.125 to 0.135×0.075 to 0.08 mm.

In *Cladorchis* Fiscoeder, 1901, the body is somewhat pyriform, flattened ventrally and convex dorsally. The anterior end is tapering, the posterior end rounded. The oral sucker has two well-developed pouches. The posterior sucker is large and ventrally situated. A genital sucker and a small cirrus-sac are present. The intestinal cæca extend to behind the testes. The latter are branched, and more or less overlapping both antero-posteriorly and laterally. The ovary and shell-gland lie mainly behind them.

C. giganteus (Diesing, 1836) is a species occurring normally in peccaries, but once recorded (perhaps as an accidental infection) from the pig, in Brazil. Its habitat is the large intestine and cæcum. It is a worm measuring 10 to 20 mm. in length, with a posterior sucker 3.4 to 4 mm. in diameter, and a genital sucker 1 to 1.5 mm. in diameter and situated at 6 to 7 mm. from the anterior end. The eggs measure 0.145 to 0.156×0.072 to 0.08 mm.

The genus *Stephanopharynx* Fiscoeder, 1901, differs from the preceding genera in the possession of a single diverticulum arising from the oral sucker. The anterior end of the worms is rather bluntly rounded. The posterior sucker is very large. The testes are placed one behind the other. *S. compactus* Fiscoeder, 1901, occurs in cattle, and also in the waterbuck (*Cobus* sp.), in Africa. This worm is 2 to 5.5 mm. long, and large specimens may be 3 mm. thick.

In *Gastrothylax* Poirier, 1883, the body is oval or somewhat elongate. The chief peculiarity of the genus, as opposed to the preceding forms,

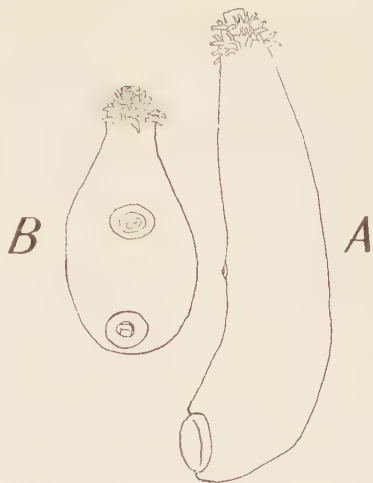


FIG. 34.—*Balanorchis anastrophus*. (AFTER LAHILLE AND JOAN, MODIFIED.)

A, lateral view of an extended specimen; B, ventral view of a contracted specimen.

is the presence of a large *ventral pouch* which opens anteriorly and extends backwards nearly as far as the posterior sucker. Into this pouch the genital ducts open. The intestinal cæca are straight, and end in front of the ovary. The uterus crosses from one side of the body to the other near the middle.

Gastrothylax crumenifer (Creplin, 1847) occurs in the ox, zebu, sheep and probably goat, in India and China, and in the buffalo in Ceylon. It

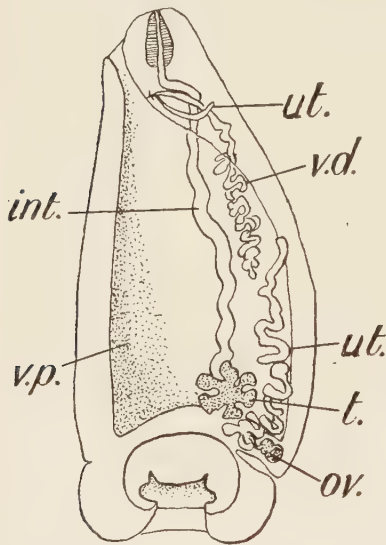


FIG. 35. — *Gastrothylax crumenifer*: RIGHT HALF OF A BISECTED SPECIMEN. (AFTER FISCHÖEDER.)

int., intestinal cæcum; ov., ovary; t., testis; ut., uterus; v.d., vas deferens; v.p., ventral pouch.

has a length of 9 to 18 mm., and a thickness of 5 mm. The eggs measure 0.115 to 0.135×0.06 to 0.07 mm. A second species, *G. compressus* Brandes, 1898, from the zebu, was recognized by Stiles and Goldberger, but Maplestone finds that so much individual variation occurs that the supposed specific characters cannot be relied upon.

Fischöederius Stiles and Goldberger, 1910, closely resembles *Gastrothylax*, possessing a similar ventral pouch, but the uterus lies in the median field of the body for its whole length, and one testis is placed dorsally to the other.

Fischöederius elongatus (Poirier, 1883) is a species measuring 10 to 20 mm. in length, which occurs in the ox, zebu, buffalo, gayal (*Palonia frontalis*) and anoa (*Anoa depressicornis*) in Ceylon, Siam, China, Java and Celebes. The eggs of this form measure 0.125 to 0.135×0.065 to 0.07 mm. According to Maplestone, several species described as distinct by Stiles and Goldberger (*F. fischöederi*, *F. siamensis*, *F. ceylonensis*) are synonyms of *F. elongatus*. These are included in the list of hosts and localities given above.

F. cobboldii (Poirier, 1883) is a somewhat smaller form, 8 to 10 mm. in length, which was originally found in the gayal in Java, but occurs also in the ox and zebu. It differs from *F. elongatus* in the greater relative length of the intestinal cæca, which terminate behind the testes, whereas in *F. elongatus* they end at about the middle of the body.

Carmyerius Stiles and Goldberger, 1910, closely resembles the last genus, but has the testes placed opposite to each other at the sides of the

body. Besides other species known only from wild animals (antelopes and hippopotamus), two forms occur in domesticated ruminants. **C. spatiosus** (Brandes, 1898), which occurs in the ox, zebu and antelopes in Africa and Arabia, is 9 to 12 mm. long, and has relatively long intestinal cæca which end behind the middle of the body. **C. gregarius** (Looss, 1896) has very short cæca, which rarely reach the middle of the body. This species measures 7 to 10 mm. in length and 2 to 2.5 mm. in thickness, and has a posterior sucker 1 to 1.5 mm. in diameter. It is a parasite of the ox and buffalo in Egypt, East Africa and India.

Gastrodiscus Leuckart, 1877, differs considerably in form from the genera already considered. The body is divided by a constriction into a small, nearly cylindrical, anterior portion and a large, discoidal, ventrally concave, posterior portion. The latter contains the genital glands, and its ventral surface is covered with regular rows of large papillæ. A ventral pouch and a genital sucker are absent. The posterior sucker is small and subterminal. The oral sucker gives off a pair of pouches. The intestinal cæca extend posteriorly behind the testes. These organs are lobate and diagonally arranged, and the ovary is behind them. The vitelline glands are mainly lateral to the intestinal cæca.

Gastrodiscus ægyptiacus (Cobbold, 1876) is a form 9 to 15 mm. in length, occurring in the small and large intestines of the horse, donkey, mule, zebra, pig and wart-hog, in Egypt, East, West and South Africa and India. In this species the genital pore is situated close to the anterior margin of the broad, posterior portion of the body, and in front of the intestinal bifurcation. The eggs measure, according to Looss, 0.17 to 0.19×0.11 mm. The intermediate hosts, in Egypt, are said to be the operculate molluscs *Cleopatra bulimoides* and *C. cyclostomoides*. After emerging from the snails, the cercariæ become encysted in water. *Gastrodiscus minor* Leiper, from the pig in Uganda, has not been described in detail, and the characters mentioned are insufficient, in Maplestone's opinion, to separate it from *G. ægyptiacus*.

Gastrodiscus secundus Looss, 1907, differs from *G. ægyptiacus* in its

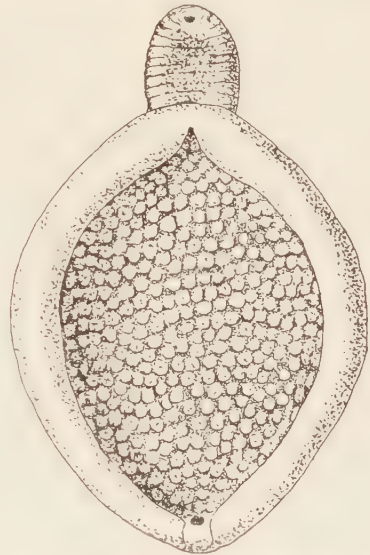


FIG. 36.—*Gastrodiscus ægyptiacus*: VENTRAL VIEW. (AFTER LEJ-TÉNYI.)

smaller size (7 to 8 × 4.5 to 5 mm.) and in the fact that the genital pore is situated much further back, behind the bifurcation of the intestine. Its eggs, according to Looss, measure 0.15 to 0.16 × 0.09 to 0.1 mm. This form was originally recorded from the intestine of mules in Assam, but is apparently of general occurrence in horses in India.

Gastrodiscus hominis (Lewis and McConnell, 1876) occurs in the colon and cæcum of man and the pig in India, Assam, Indo-China and the Malay States. It has also been recorded from the mouse-deer (*Tragulus*). The pig is probably its natural host. It is of a reddish colour when fresh, and measures 6 to 8 × 3 to 4 mm. The eggs measure 0.15 × 0.072 mm. Leiper, in 1913, proposed the genus *Gastrodiscoides* for this species. The validity of the genus is still *sub judice*, the distinction having been based on characters that appear to be subject to great variation in worms preserved in different states of contraction.

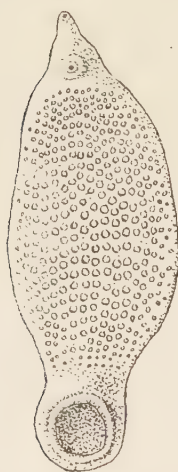


FIG. 37.—*Homalogaster paloniæ*: VENTRAL VIEW. (AFTER POIRIER.)

Homalogaster Poirier, 1883, is a singular form in which the body is divided into a large, flattened, anterior portion, containing the genital glands, and a much smaller posterior portion which bears the posterior sucker. The dorsal surface of the anterior portion is convex, its ventral surface flat or concave and covered with longitudinal rows of large papillæ. The genital pore is situated on a protrusible papilla, but is without a sucker. The oral sucker gives off a pair of pouches. The intestinal cæca extend behind the testes, and the ovary is situated behind these organs.

Homalogaster paloniæ Poirier, 1883 (of which *H. poirieri* Giard and Billet, 1892, and *H. philippinensis* Stiles and Goldberger, 1910, are regarded by Maplestone as synonyms), occurs in the large intestine of domesticated cattle in Asia (Siam, Java, China and the Philippines), as well as in the gayal.* It measures 7.5 to 12 mm. in length and 4.5 to 6 mm. in width. The diameter of the posterior sucker is 2.5 to 3 mm. The eggs measure 0.125 to 0.139 × 0.067 to 0.086 mm., and have a small knob at the pole opposite to the operculum.

ii. THE TAPEWORMS OR CESTODES (CLASS CESTOIDEA).

Brief definition.—Flatworms in which the body is either unisegmental or, more commonly, segmented (strobilate), and is without a cellular

* The writer has also seen specimens which were said to have been obtained from a sheep at Hong-Kong.

epidermis or external cilia. All members of the group are internal parasites of other animals. An alimentary canal is absent.

The general form of the body in the Cestodes is flattened, elongate and ribbon-like as a rule, though a few forms are more or less cylindrical.

The class is primarily divided into two groups (termed by Poche "Subsubclasses"):

(1) **Amphilinoinei**, containing only forms with an unsegmented, or rather unisegmental, body.

(2) **Tænioinei**, including all the forms which are important for our present purpose. The majority of this group are segmented.

The Tænioinei are subdivided into four orders, **Bothriocephalidea**, **Echinobothriidea**, **Tetrarhynchidea** and **Tæniidea**. Of these only two, the **Bothriocephalidea** and the **Tæniidea**, require consideration here. The order **Bothriocephalidea** includes nine families, of which we are only concerned here with one, the **Diphyllobothriidæ**.

Most of the Cestodes of man and the domestic animals belong to the order **Tæniidea**. Of this order, six families, comprising forms which occur chiefly in fishes, are placed in a suborder **Phyllobothriinea**. The remaining eleven families form the suborder **Tæniinea**, with which alone we have to deal in the present work.

General Characters of Segmented Cestodes.

The individual worm consists of a "head" or scolex, situated at what is usually spoken of, for convenience, as the anterior end, and a chain (strobila) of segments, or proglottides. The scolex is usually provided with clinging organs in the form of suckers. In the **Bothriocephalidea** these organs, when present, take the form of a pair of slit-like "bothria," situated dorsally and ventrally. In the **Tæniidea** there are almost invariably four muscular organs, two dorsal and two ventral, which may take the form of large, thin, prominent, folded flaps or "bothridia," or (more commonly, and in all the forms with which this work deals) sessile or not very prominent, cup-like, circular or oval suckers. In addition, in a large number of the **Tæniinea**, the scolex is provided with a median, muscular, proboscis like and frequently retractile organ known as a rostellum, which is generally armed with chitinous hooks, forming an additional means of attachment to the host. In some cases the suckers, or even part of the general surface of the scolex, may also be armed with small hooklets or spines.

The strobila shows a regular progression in the stage of development of the segments from those nearest to the scolex to those furthest away from it. Young segments are, as a rule, continually added, throughout the life of the worm, immediately behind the scolex, or are differentiated

from the hinder end of a short unsegmented portion, or "neck," which follows the scolex. As they pass back along the strobila the segments become first "mature" by the development of their sexual organs to a functional condition, and eventually "gravid," by the development of a uterus or other structure containing fertilized eggs, and the disappearance of most of the other organs. The gravid segments are usually shed, one or several at a time, in succession from the posterior end, and are passed out with the host's faeces. The eggs may escape from them either before or after this occurs.

The musculature of the strobila consists mainly of continuous longitudinal fibres arranged in more or less definite bundles which may be in one or more concentric layers. The bulk of these longitudinal muscles is situated rather deeply in the parenchyme, and immediately below them there is usually a thin layer of transverse fibres. This layer is generally regarded as the dividing-line between the "cortical" or outer portion of the parenchyme and the "medullary" or inner portion. In addition, there are frequently a few fibres running dorso-ventrally through the parenchyme, while immediately below the cuticle there are also thin layers of longitudinal and transverse fibres.

The "brain," consisting of a more or less complex system of intercrossing nerve-fibres and ganglionic cells, is situated in the scolex, and there is usually a single pair of main longitudinal cords of nerve-fibres proceeding from this and running throughout the strobila. The collecting apparatus of the excretory system consists typically of two pairs of lateral longitudinal canals, one dorsal and one ventral, each continuous throughout the strobila. The ventral canals are usually of wider calibre than the dorsal canals, and are, as a rule, connected at the back of each segment by a transverse vessel. In exceptional cases the longitudinal excretory canals are more numerous, or may even form a complex network. Occasionally the dorsal pair is absent. The various longitudinal canals are all in communication with each other anteriorly by means of transverse commissures situated in the scolex. Posteriorly they sometimes empty into a small terminal bladder, which is, of course, lost at the shedding of the first segment.

Though there are very rare instances of bisexuality among Cestodes, the general rule is that each mature segment contains one or two complete sets of both male and female organs, and may, for practical purposes, be compared in this respect with one of the hermaphrodite Trematodes. The male and female genital ducts may open separately, or (more commonly) into a common "genital atrium," and their openings may be either on one of the flat surfaces (the "ventral" surface) of the segment or on one of its lateral margins. In the Bothriocephalidea the pores are

frequently ventral, in the Tæniidea they are almost invariably lateral. A separate uterine pore, for the escape of eggs from the gravid segments, is only exceptionally present, and even when present is sometimes not a permanent structure, but a mere temporary dehiscence of the wall of the uterus and of the body-wall. As a general rule, in the Tæniidea, the eggs only escape by the disintegration of the gravid segments.

There may be only a single testis or, more usually, a number of testes, discharging their spermatozoa into fine ducts (*vasa efferentia*) which join to form a *vas deferens*. This may be expanded so as to form one or more seminal vesicles, and opens to the exterior through a *cirrus*, contained within a muscular *cirrus-sac*. Instances of self-fertilization in individual segments are frequently observed, and this process may be rather the rule than the exception, as the vagina usually opens in immediate proximity to the *cirrus-sac*.

The vagina frequently has an expansion in its course, forming a *receptaculum seminis*. At its inner end it is connected with the oviduct, or with an "oötype," with which are also connected the shell-gland and the vitelline gland or glands. The ovary is single, though it may be more or less distinctly bilobed, or may consist of a number of radiating finger-like lobes. The vitelline gland is a single, compact organ in the majority of the Tæniidea, but consists of numerous separate follicles in some members of this order and in the Bothriocephalidea. The uterus is formed at first as a tubular outgrowth from the oviduct, and may be a persistent or a temporary structure. In the former case it may assume a variety of shapes in different families and genera, being either sac-like, pouched, branched or reticulate. In the latter case it disappears at an earlier or later stage, and is replaced either by an organ formed of dense, fibrous parenchyme, known as a *paruterine organ*, or by a number of parenchymatous capsules, each enclosing one or several eggs, and conveniently termed *egg-capsules*.

The eggs, before laying, are usually enclosed in two membranes, of which either may be thickened and of a chitinous nature, forming a definite "shell." The embryo, when fully formed, is a spherical or ovoid mass of cells provided at one pole with (usually) three pairs of hooks, which it is able to use as levers either in simple locomotion or in burrowing into its host's tissues. It is frequently referred to as a "hexacanth embryo" or "onchosphere." In the Bothriocephalidea, so far as their life-history has been studied, the embryo is ciliated externally, and hatches in water, where it is able to swim by means of its cilia. In other forms the hexacanth embryo hatches only when the egg is ingested by a suitable host. In all Cestodes the life-history involves a more or less complex

metamorphosis, and in almost all of them one or more changes of host. These matters will be more conveniently discussed in dealing with the groups individually.

DIPHYLLOBOTHRIDÆ.

The order **Bothriocephalidea** includes, according to Poche's classification, five tribes, four of which consist of forms occurring in fishes, etc., and not of importance from the medical or veterinary point of view. The forms with which we are here concerned all belong to the tribe *Diphyllbothrioidæ* and to the family *Diphyllbothriidæ*.

The tribe *Diphyllbothrioidæ* consists of forms in which the strobila may or may not be obviously segmented—*i.e.*, the external segmentation may be distinct or may be very faintly or not at all indicated. Internally, however, the adult forms always show a longitudinal series of distinct sets of genital organs. The scolex is generally unarmed, and is provided with a pair of groove-like, slit-like or tubular organs ("bothria") functioning as suckers. These are in reality situated on the dorsal and ventral surfaces, but the scolex is frequently laterally compressed (*i.e.*, compressed in a plane at right angles to the flat surfaces of the strobila), and when this is the case it often tends to be twisted round so that it appears to lie in the same plane as the rest of the worm, the bothria then appearing to be laterally placed.

The genital pore (common pore of cirrus and vagina) is situated on the ventral surface of the segment, near the median plane of each set of genital organs. The vitelline glands are diffuse, and situated in the cortical parenchyme. A cirrus-sac, with a muscular wall, is present. There is a large receptaculum seminis. In addition to the usual genital pore, and independent of the vaginal opening, there is a *uterine pore* through which eggs escape from the uterus. The eggs are thus shed gradually, before the separation of the gravid segments from the strobila. The eggs are thick-shelled, more or less ovoid in shape, and provided with an operculum at one pole, like the eggs of the digenetic Trematodes. The embryo is not formed before the deposition of the eggs.

In the family *Diphyllbothriidæ* the bothria typically have the form of shallow grooves, though in certain genera they may, by the fusion of their margins, become tubular. Each segment contains either one or two sets of genital organs and corresponding genital and uterine pores. The uterine pore is situated behind the genital opening. The uterus is a coiled tubular structure, its coils and loops sometimes forming a "rosette." The testes are usually numerous, and are situated laterally and dorsally in the medullary parenchyme.

The family contains about thirteen genera, whose species occur, as adults, in the intestine of mammals, birds and reptiles. The life-history

of these forms is completely known only in a few cases. So far as is known, all Diphyllobothriids require at least one intermediate host, which is a vertebrate, and in whose tissues the larval form occurs as a ribbon-like creature not unlike the adult, but less elongate, unsegmented, and with genital organs as yet undeveloped. This type of larva is generally known as a *plerocercoid*. For those species which have been most fully studied, it has become known comparatively recently that there is an earlier larval stage which occurs in Copepod Crustacea. The life-history of these forms will be more conveniently considered in dealing with the genus *Diphyllobothrium*.

In *Diphyllobothrium* Cobbold, 1858 (= *Dibothriocephalus* Lühe, 1899) the scolex is relatively small, but usually distinct, generally somewhat ovoid in shape, and provided with fairly well developed, elongate, groove-like bothria. The strobila is often of great length, and contains a very large number of well-defined segments. In each of these there is a single set of genital organs. The testes and vitelline glands are mainly confined to two lateral fields, but these may extend towards the middle line or even coalesce near the anterior or posterior border of the segment. The other organs lie in the median field, the genital pore and cirrus-sac being somewhat anteriorly placed, in or near the middle line, with the uterus and its pore behind them. Behind the uterus and towards the posterior margin of the segment is the bilobed ovary, and behind this again the shell-gland. The cirrus-sac is placed with its long axis vertical to the flat surfaces of the segment. The posterior segments, after shedding their contained ova, become very much attenuated, and are finally lost and passed out with the host's fæces.

The adult forms of *Diphyllobothrium* occur in mammals and birds, and several species have been described as occurring in man and certain domestic animals (cat and dog). Unfortunately these species are, for

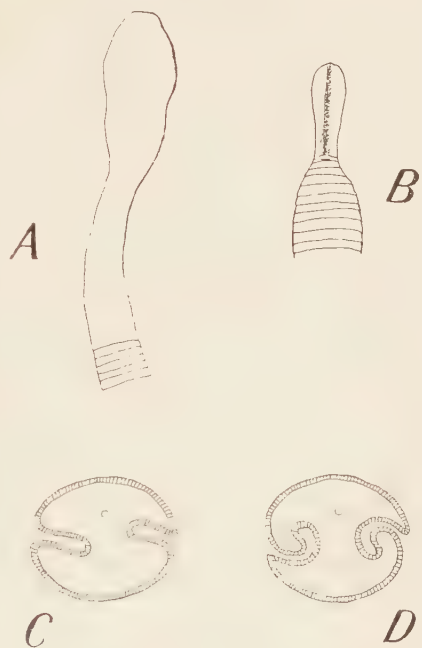


FIG. 38. *Diphyllobothrium latum*:
SCOLEX. (AFTER STEIN.)

A, lateral view; B, dorsal view; C, D, transverse sections at different levels.

TABLE I.—SPECIES OF *DIPHYLLOBOTHRUM* OCCURRING AS ADULTS IN MAN AND DOMESTIC ANIMALS.*

Species.	Length of Strobila in Cm.	Maximum Width of Strobila in Mm.	Position of Genital Pore.	Cirrus-Sac.	Approximate Number and Arrangement of Testes.	Uterine Loops on Each Side of Middle Line.	Enlargement of Uterus.	Size of Eggs in μ .	Hosts of Adult Form.	Geographical Distribution.
<i>D. latum</i> (Linnaeus, 1758)	200 to 2,000	20	At about anterior quarter of segment	Extends half-way to dorsal surface	750 to 800, in two distinct lateral fields	About 4 to 8, extending forward at sides of genital pore	Absent	67 to 70 $\times$ 45 to 54	Man, dog, cat, wild carnivores	Asia, Africa, N. America.
<i>D. cordatum</i> (Leuckart, 1863)	80 to 115	5 to 10	Near anterior margin of segment	0.6 $\times$ 0.43 mm.	240 to 300, in two distinct fields	6 to 8, extending forward at sides of genital pore	—	70 to 80 $\times$ 50	Dog, seals, walrus, rarely man	Greenland, Iceland.
<i>D. fuscum</i> (Krabbe, 1865)	0.8 to 80	5	Slightly in front of middle of segment	—	—	5 to 15, extending forward at sides of genital pore	Absent	Length 55 to 60	Dog	Iceland.
<i>D. decipiens</i> (Diesing, 1850)	About 150	About 8	—	Extends half-way to dorsal surface	—	—	—	Length 50 to 60	Cat, dog, wild carnivores	Europe, Asia, America (?).
<i>D. mansoni</i> (Cobbold, 1882)	10 to 250	5 to 12	Slightly in front of middle of segment	—	380 to 540, not in distinct lateral fields	3	Absent	59 to 76 $\times$ 31 to 44	Cat, dog, wild carnivores, [man]	Asia [? N. and S. America, E. Africa, Australia].
<i>D. railleii</i> (v. Rátz, 1913)	45 to 52	7	Near anterior margin of segment	Extends more than half-way to dorsal surface	300 to 500, in two distinct fields	6 to 7	Present	67 to 72 $\times$ 40 to 54	Dog	E a s t e r n Europe.
$\dagger D. reptans$ (Diesing, 1854)	100	9	At anterior quarter of segment	Extends half-way to dorsal surface	144 to 220, in two distinct fields	in 4, not extending forward at sides of genital pore	Present	53 to 59 $\times$ 36 to 40	Dog	S. America, Burma.
$\dagger D. ranarum$ (Gastaldi, 1854)	113	5	Near anterior margin of segment	—	200 to 220, in two distinct fields	in 3 to 5, extending forward at sides of genital pore	Present	58 to 67 $\times$ 34 to 36	Dog	Burma.

* Certain other supposed, but imperfectly known, species found in man, dog, and cat are omitted from this table, on the ground that they are probably synonyms of one or other of the species mentioned. *D. americanum*, Hall and Wigdor, 1918, from the dog in the United States, appears to be known only from immature specimens, and Hall states that the dog is probably an abnormal host for the species.

† These specific names are applied by Meggitt to adult forms obtained by him experimentally in dogs, after feeding with forms of "*Sparganum*." "*S. reptans*" is a larval form recorded from a large number of vertebrates (amphibia, reptiles, birds, and mammals), mainly South American. The form used in Meggitt's experiment was found in a snake (*Tropidonotus* sp.) in Burma. Meggitt's specimens of "*Lagula ranarum*", which gave rise experimentally to the adult form which he names *Diphyllobothrum ranarum*, were found in the wall of the stomach of a Burmese frog (*Rana tigrina*). In this form the larva is apparently capable of asexual multiplication by transverse fission. In view of the widespread occurrence of forms of "*Sparganum*" in a great variety of hosts, and the difficulty of distinguishing between them in the immature condition, specific identification based upon the host must be accepted with caution.

the most part, very ill defined, and it is a matter of considerable difficulty to find satisfactory morphological characters for separating them. Some of the characters of the more important of the supposed species are given in Table I. It is impossible, however, in the present state of our knowledge, to draw up specific definitions, or even a key, which would enable any given adult form met with in a domestic host to be assigned with certainty to its species. Of the characters mentioned in the table many appear to be so variable as to be quite unreliable, and it seems possible that several of the supposed species may ultimately be found to be synonyms.

The best-known form is **Diphyllobothrium latum** (Linnæus, 1758), whose normal definitive host is probably man (specimens obtained experimentally in dogs and cats are usually smaller than those found in

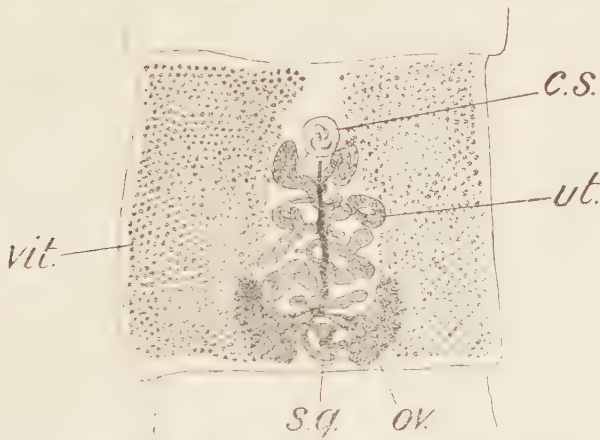


FIG. 39. *Diphyllobothrium latum*: MATURE SEGMENT. (AFTER STEPHENS.)
c.s., cirrus-sac; ov., ovary; s.g., shell-gland; ut., uterus; vit., vitellaria.

man). In this species the strobila attains a great length and may contain from 3,000 to 4,000 segments. The scolex is almond-shaped and measures 2 to 3 mm. in length. The colour of the worm, when fresh, is reddish or yellowish grey, with a dark central patch (caused by the ova in the uterus) in each of the posterior segments. This species is probably of world-wide occurrence, though it is mainly known in Europe, and especially in Switzerland and on the shores of the Baltic. It has also been recorded from various localities in Asia and Africa, and from the region of the Great Lakes in North America. Besides man, its definitive hosts are said to include the dog, cat, fox, seals, the polar bear, porpoise, etc.—all of which are, or may be, fish-eaters.

The life-history of this form is now completely known, thanks to the researches of Janicki, Rosen and others. It had been known for many

years that infection was acquired by the definitive hosts through eating fish, and the later larval stage (plerocercoid) had been recognized in fishes. The ciliated embryo which hatches from the egg was also known, but its connection with the plerocercoid, and the means by which the fish became infected, were not understood until the publication, in 1918, of the work of Janicki and Rosen. Briefly, the life-history is as follows. The eggs, when laid, do not contain fully-formed embryos. They pass out of the definitive host's body with the fæces, and the hexacanth embryo is not developed until a few weeks or months (according to temperature and other conditions) after they have reached the exterior. This embryo, on

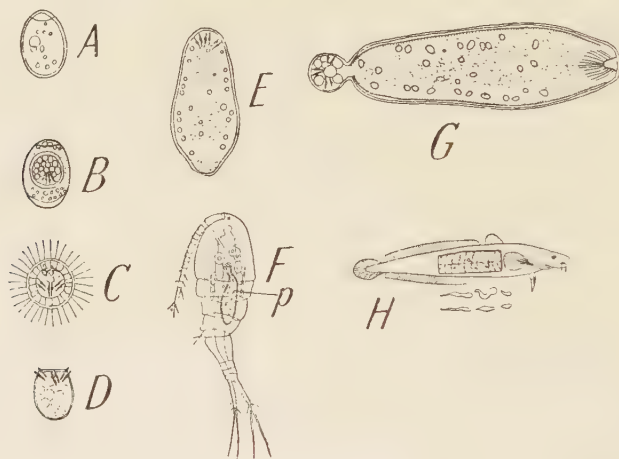


FIG. 40.—*Diphylobothrium latum* : DIAGRAM OF LIFE-HISTORY.
(AFTER BRUMPT, MODIFIED.)

A, egg as found in faeces of final host; B, egg after development of embryo; C, ciliated embryo (coracidium); D, embryo after ingestion by copepod and loss of ciliated coat; E, embryo after reaching body-cavity of copepod; F, proceroid (*p.*) in body-cavity of copepod; G, the same, removed from its host; H, plerocercoids in muscles of fish. (Below, some of these are shown on a larger scale.)

NOTE.—The scale of magnification is not uniform for all the figures.

hatching in water, is a spherical organism covered with a coat of long cilia, and sometimes called a *coracidium*. It may swim about by means of its cilia for several days, but usually dies after a few hours unless it is ingested by one of the appropriate first intermediate hosts. These are Copepod Crustacea (Entomostraca), or “water-fleas” (in Europe, *Cyclops strenuus*, *Diaptomus gracilis*; in America, according to Essex (1927), *Cyclops brevispinosus*, *C. prasinus*, *Diaptomus oregonensis*). Making its way into the body of the Copepod, the young larva develops into a stage which has been named the *proceroid*. After two or three weeks this reaches its full development and is infective for the second host. It is now

an organism of somewhat elongate form, about 0.5 mm. long, with a protrusible proboscis-like structure at one end and a spherical appendage, containing the six original embryonic hooks, at the other. The cuticle is armed with small spines, which disappear later.

When the Copepod is swallowed by a suitable fish, the procercoid loses its posterior appendage, bores through the wall of the fish's intestine and settles in some organ or tissue, such as the liver or musculature, where it grows into a plerocercoid, ultimately measuring about 10 to 20 mm. in length. It is now ready to infect the final host, and should the fish be eaten in the raw state, or after insufficient cooking, the young worms establish themselves in the intestine and reach maturity in about five or six weeks. The plerocercoids are readily killed by a temperature of 50° C. or over, and boiling the fish for ten minutes is sufficient, according to Brumpt, to prevent human infection. A frequent source of infection, in some localities, is said to be the consumption of raw caviare made from the roe of the pike.

Fuhrmann has observed cases of apparent multiplication of the plerocercoids in the fish host, and believes that they may undergo a phase of asexual multiplication by fission.

Among the fishes in which the plerocercoids of *D. latum* occur (in Europe) are the pike (*Esox lucius*), perch, trout, salmon, grayling (*Thymallus*), *Lota vulgaris* and species of *Coregonus* and *Acerina*. In Japan, *Oncorhynchus perryi* has been implicated. In North America, Vergeer has recently recorded the occurrence of the plerocercoids in *Stizostedion canadense-griseum*, *S. vitreum*, *Esox lucius* and *Lota maculosa*.

Diphyllobothrium cordatum (Leuckart, 1863) is a smaller form than *D. latum*, and occurs in the dog, walrus and seals in Iceland and Greenland. It has been recorded once as a parasite of man in the latter country. It has a broad, flattened scolex, heart-shaped in outline, and measuring about 2 mm. in length and the same in width, and the strobila has from 400 to 600 segments. There is a dorsal and a ventral longitudinal groove running along the strobila, the genital pores being situated in the ventral groove. The intermediate hosts are unknown, but the plerocercoid almost certainly occurs in fishes.

Diphyllobothrium parvum (Stephens, 1908) is said to differ from *D. latum* in the smaller size of its gravid segments, which are only 3 mm. wide, as against 10 to 12 mm. or more; in the smaller dimensions of the mature segments (4 × 4 mm., as against 6 × 6 mm.); and in the smaller size of the eggs. This species was originally described from fragments of strobila obtained from a native of Syria who had lived for a short time in Tasmania. It has since been recorded from various other parts of the world.

Diphyllobothrium mansonii (Cobbold, in Manson, 1882) was known for many years in the late larval stage, under the name of *Sparganum mansonii*, before its adult form was discovered. The larval form, which was first described from the peritoneum and abdominal cavity of man in China, is a large plerocercoid which may attain a length of 8 to 36 cm. and a width of 3 to 12 mm. It occurs in the connective tissue of the vertebrate intermediate hosts, which apparently include, besides man, many other animals (frogs, snakes, birds, rats, monkeys, etc.). Japanese investigators have found that the adult form is a typical *Diphyllobothrium*



FIG. 41.—*Diphyllobothrium mansonii*: SCOLEX, DORSAL VIEW. (AFTER FAUST.)

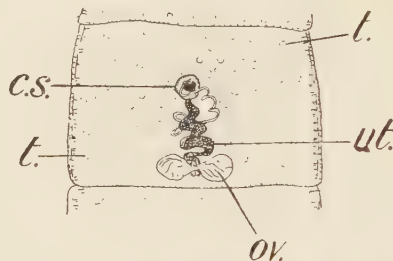


FIG. 42.—*Diphyllobothrium mansonii*: MATURE SEGMENT. (AFTER FAUST.)

c.s., cirrus-sac; ov., ovary; t., t., testes; ut., uterus.

occurring in the intestine of the cat and dog, while Okumura has demonstrated that the life-history is similar to that of *D. latum*, the procercoid stage occurring (in Japan) in the Copepod *Cyclops leuckarti*.

The eggs are relatively more elongate and more pointed at the poles than those of *D. latum*. Though known mainly from China and Japan, the species probably has a very wide distribution.*

Sparganum (*Gatesius*) **proliferum** (Ijima, 1905) may appropriately be mentioned here. This is a remarkable immature form known only from

* It should be borne in mind that "*Sparganum*" is merely a name for an artificial group of larval forms of the type of "*S.*" *mansonii*, which are simply large plerocercoids. There are at present no means of distinguishing specifically between larvæ of this kind, unless the adult forms can be obtained by feeding experiments, and it is unsafe to assume that they are specifically distinct because they occur in different hosts or in different geographical regions. There appears, for example, to be nothing at present to distinguish *S. barteri* Sambon, 1907, from *S. mansonii*. This form was described as a distinct species on account of its occurrence in a native of East Africa. In the case of *S. railletii* v. Rátz, 1913, from the pig in Eastern Europe, there is, perhaps, slightly more justification for the specific distinction, since Kotlán has obtained the adult experimentally in the dog, and according to his description it appears to show certain slight differences from the adult of *D. mansonii* (see Table I). Kotlán failed to infect himself by swallowing a plerocercoid of *D. railletii*, but it would probably be unwise to argue from this fact that the species is distinct from *D. mansonii*, the adult form of which has only been recorded once in man.

man in Japan and Florida. It occurs in subcutaneous cysts, and is very variable in form. It may be elongate and ribbon-like, in which case it may attain a length of 12 mm. and a width of 2.5 mm., and has an apical depression at the anterior end, but no recognizable bothria; or it may assume an irregularly branching appearance, owing to the formation of



FIG. 43.—*Sparganum baxteri*. (FROM CASTELLANI AND CHALMERS, AFTER SAMBON.)

a number of lateral "buds." Its most remarkable peculiarity is the fact that it appears to be capable of asexual multiplication in the larval stage, the "buds" becoming separated from the main mass and wandering away into other situations. In this way large numbers of encysted larvæ may become scattered about in the host's subcutaneous tissues, giving



FIG. 44.—*Sparganum proliferum*. (AFTER STILES.)

rise to considerable pain and distress. The adult form and definitive host are unknown. Presumably there are other intermediate hosts besides man, and the adult occurs in some carnivorous mammal, or possibly a bird or reptile. Stiles, in 1908, proposed the "subgeneric" name *Gatesius* for this form, on account of its striking differences from other forms of "*Sparganum*."

In the genus **Diplogonoporus** Lönnberg, 1892, the scolex is relatively short, but has two powerful, groove-like bothria. The numerous segments of the strobila are short but very broad, each containing two sets of genital organs. In each segment may be recognized a median field, two uterine fields and two lateral fields. The genital and uterine pores lie in a longitudinal row in each uterine field. The vitelline glands and the testes lie in the lateral and median fields, the former between the outer and inner layers of longitudinal muscles. The loops of the uterus form a "rosette." The adult forms of this genus occur in the intestine of whales, seals and man.

Diplogonoporus grandis (R. Blanchard, 1894) is a very large form, measuring sometimes as much as 10 metres in length and having a maximum width of about 25 mm. According to Yoshida and Takano the scolex (which was missing in Blanchard's original specimen) is funnel-shaped, or like a half-unfolded fan, and measures 1.1 mm. in length and 1 mm. in width. The edges of the bothria overlap to form a canal, except in front, where the groove is open. The genital and uterine pores lie in two parallel longitudinal grooves on the ventral surface. The eggs have a thick brown shell and measure 0.063×0.048 to 0.05 mm.

About seven cases of human infection with this worm have been recorded in Japan, the persons affected being sometimes known to have lived near the sea and to have been in the habit of eating raw fish. Though the life-history is unknown, it is extremely probable that the intermediate hosts are fishes and that not only man, but other fish-eating mammals, serve as definitive hosts.

Diplogonoporus brauni Léon, 1907, is a closely related form recorded on more than one occasion from the intestine of man in Roumania. It is described as having a length of 29 cm. and a width of 6 mm. The scolex is 1 mm. long, and is not distinct from the strobila. The bothria are narrow. There are two longitudinal grooves both dorsally and ventrally running throughout the strobila, those on the ventral surface being deeper and containing the genital openings. The posterior segments, when empty of eggs, become very narrow again, so that the two ends of the worm appear very much alike.

Braunia Léon, 1908, is a remarkable form considered to belong to the subfamily Ligulinae,* on account of the incomplete nature of its segmentation. There is little or no trace of segmentation externally, though internally segmentation is well-marked. The anterior end is blunter than the posterior, and a dorsal and a ventral furrow run throughout the whole length of the worm.

* *Ligula*, the typical genus of this group, occurs as an adult in the intestine of fish-eating birds, and the plerocercoid occurs in fishes.

Braunia jassyensis Léon, 1908, was described from a single specimen, in which the genital organs were apparently not fully developed, obtained from the intestine of man in Roumania. The length of the worm was 18 cm., and its maximum width 12 mm. The peripheral musculature is described as consisting of three layers, one of transverse fibres between two of longitudinal. The numerous testes are arranged in two layers on the dorsal side of the medullary parenchyme, and the vitelline glands lie between the outer (subcuticular) muscles and the longitudinal muscles. Léon considers that this form differs from other *Ligulinæ* in the form and extent of the ovary.

The order **Tæniidea** consists of strobilate Cestodes in which the scolex may be armed with hooks or unarmed, but is almost always provided with four suckers or more elaborate sucker-like organs known as bothridia. The external segmentation of the strobila is usually well marked. There may be either a single set of genital organs in each segment, or two sets, with corresponding genital pores. A preformed uterine pore is almost always absent. The uterus is of very variable form. It is most commonly sac-like or branched, but in some genera it is replaced by separate parenchymatous structures variously known as egg-capsules or as paruterine organs, each of which may contain one or several eggs. The egg-shells are without an operculum, and the embryos are developed within them before deposition.

The order contains, according to Poche's system, two suborders, *Phyllobothriinea* and *Tæniinea*. The former group, which closely corresponds with the order *Tetraphyllidea* of many authors, consists of forms chiefly parasitic in the lower vertebrates, especially in fishes. All the forms of interest for our present purpose belong to the suborder *Tæniinea*, which corresponds, in the main, with the order *Cyclophyllidea* of the older classifications.

In the **Tæniinea** segmentation is almost always complete, and the strobila may contain only a few segments, or a large number. The scolex may or may not be provided with a rostellum. When present, the rostellum is occasionally unarmed, but is more often armed with one, two, or several transverse crowns of hooks. The suckers may also be armed or unarmed. The genital pores are usually situated on the lateral margins of the segments. The reproductive organs, of which there may be a single or a double set, are situated in the medullary parenchyme. The testes may be few (occasionally only one) or numerous in each segment. The vitelline gland is a single, compact organ (though sometimes divided into two more or less distinct lateral portions), situated behind the ovary. The uterus is either persistent or is replaced sooner or later by egg-capsules or by structures known as "paruterine organs," consisting

of modified parenchyme, in which the eggs become embedded. The segments become detached from the strobila, as a rule, before shedding their contained eggs, and the eggs are finally liberated by the dehiscence of the walls of the segments.

The adult worms are parasitic in vertebrates. The larval stages (known as cysticerci or bladderworms) occur among the tissues or viscera, or in the body-cavity, of animals of almost every class. The life-history, in almost all known cases, involves a change of host before sexual maturity can be attained. In a few cases, however, it is now recognized that the larval form is capable of living in the same host-species as the adult, so that an intermediate host, in the usually accepted sense, is not required. But even in these instances it is probably always necessary for the eggs

to reach the exterior and to be ingested either by the same or another host-individual.

The type of larval Cestode known as a **Cysticercus** has a scolex with four adhesive organs in the form of typical "suckers" as distinct from the *bothria* or *bothridia* met with in other forms. Typically a thin-walled caudal bladder is present, filled with fluid, into which the scolex may be invaginated. This is the form of larva especially typical of the family Tæniidæ. Other forms of *Cysticercus* may be recognized as follows:

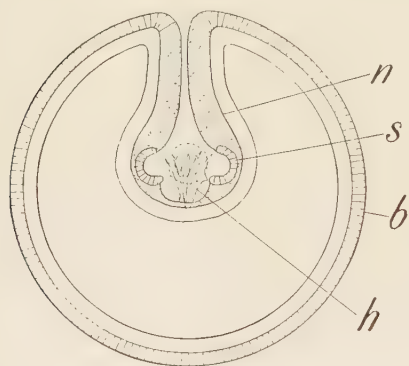


FIG. 45.—DIAGRAM OF A CYSTICERCUS.
(ORIGINAL.)

b., bladder; h., hooks; n., neck; s., sucker.

Dithyridium (or *Piestocystis*) (by some authors called a Plerocercoid, but this term is perhaps better reserved for the larvæ of Bothriocephalidea).—This is a more or less elongate form with a solid body and without a caudal bladder. The scolex is invaginated into the body in such a way that its apex forms the bottom of the invagination—when invaginated, it is, in fact, inside out. The caudal portion of the larva is either not distinct from the scolex or is only distinguished by its greater opacity.

Cysticercoid.—The scolex is withdrawn in its natural position (not inverted) into the interior of the larva, and is surrounded by a double fold of integument, whose outer layer, corresponding to the "caudal bladder," forms a more or less spherical cyst (which is sharply set off when the scolex is evaginated), while the inner layer, in the evaginated condition, forms a "neck" connecting the cyst with the scolex. Cysticercoids occur in a variety of forms. There may be a tail-like appendage, sometimes as long as or longer than the body, and usually containing the

six original embryonic hooks. This appendage represents the wall of the original hexacanth embryo (sometimes called the "blastogene"), and the rest of the larva is formed as an out-growth from it. This tailed form of larva is called a **Cercocystis**. It is typical of the genus *Hymenolepis*, among others. Sometimes the cyst becomes separated from the appendage on reaching its full development, and the larva is then known as a **Cryptocystis**. This is the type of cysticercus met with, for example, in the genus *Dipylidium*.

In other forms (e.g., *Davainea proglottina* and some *Hymenolepididæ*) the cyst is formed within the "blastogene," which thus forms an outer investment. In others, again (e.g., *Anomotania*), the "blastogene" apparently forms a closed cyst within which the larva lies free. This type of cysticercoid is called a **Mono-cercus**. Occasionally several such larvæ are formed within one "blastogene." To this condition the name **Polycercus** has been given.

There are other modifications in the form and mode of development of the cysticercus which have received special names, but these need not be discussed here.

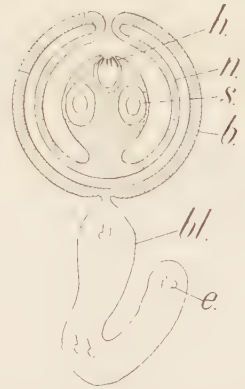


FIG. 46. — DIAGRAM OF A CYSTICERCOID (*Cercocystis* TYPE). (ORIGINAL.)

b., bladder; *bl.*, "blastogene"; *e.*, embryonic hooks; *h.*, definitive hooks; *n.*, neck; *s.*, sucker.

MESOCESTOIDIDÆ.

The family **Mesocestoididæ**, represented by the genus **Mesocestoides** Vaillant, 1863, appears to occupy a position intermediate between the Bothriocephalidea and the more typical of the Tæniidea, though the resemblance to the former may perhaps be more apparent than real. In *Mesocestoides* the scolex is without rostellum or hooks, and the four suckers are oval, unarmed, and have a wide, longitudinally elongate aperture. There is a single set of genital organs in each segment. The genital pores are situated near the middle line of the ventral surface, the vagina opening in front of or beside the cirrus-sac. The uterus is an elongate sac, irregularly constricted, lying longitudinally in or near the median line of the segment. It curves round the cirrus-sac anteriorly, and when fully developed its posterior portion becomes modified into a large, single egg-capsule with a thickened parenchymatous wall, in which most of the eggs are accumulated.

Mesocestoides lineatus (Goeze, 1782) occurs in the small intestine of the dog, cat and various wild carnivorous mammals in Europe and Africa. It has a relatively large scolex, somewhat flattened in front, and with a slight apical depression. The strobila attains a length of 30 to 250 cm., and when fresh is faintly reddish along the middle line. The maximum width is about 3 mm. Each mature segment contains fifty or more large testes, which extend on both sides of the longitudinal excretory canals. The cirrus-sac is anteriorly placed. The ovary and vitelline gland are both divided into two distinct lateral lobes, and lie near the hinder margin of the segment. The eggs are oval, and provided with two thin envelopes. They measure 0.04 to 0.06×0.035 to 0.043 mm.

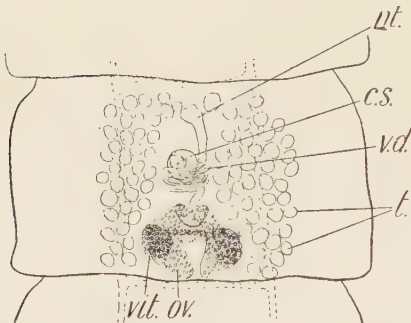


FIG. 47. — *Mesocestoides lineatus*: MATURE SEGMENT, DORSAL VIEW. (ORIGINAL.)

c.s., cirrus-sac; ov., ovary; t., testes; ut., uterus; v.d., vas deferens; vit., vitellarium.

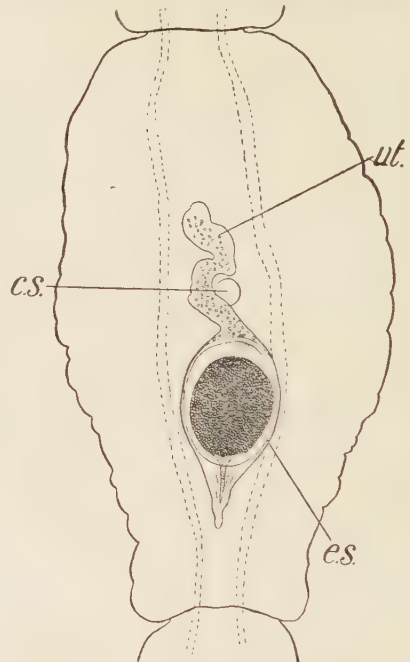


FIG. 48. — *Mesocestoides lineatus*: GRAVID SEGMENT, DORSAL VIEW. (ORIGINAL.)

c.s., cirrus-sac; e.s., egg-sac; ut., uterus.

It is doubtful whether *M. litteratus* (Batsch, 1786), which has been recorded from the dog, fox, jackal, wild cat and other carnivores, can be regarded as a distinct species from *M. lineatus*.

The life-history and intermediate hosts of *Mesocestoides* are not satisfactorily known. The type of larval Cestode known as *Dithyridium* (or *Piestocystis*) (see p. 76) has a scolex which suggests its connection with this genus. Moniez, in 1880, suggested that "*Dithyridium*" *lacertæ* Valenciennes, found in lizards, was the larval form of a species of *Mesocestoides* (*M. perlatus* Goeze) which occurs in various birds of prey. Alessandrini, in 1907, described a "*Dithyridium*" from the lungs of the

fowl (which he believed to be identical with the "*Piestocystis variabilis*" of Diesing, from the rook and other wild birds), and thought it probable that it was the larva of *M. lineatus*. On the other hand, Cholodkovsky, in 1917, described quite a different kind of larva (a true cysticercus), with an unarmed scolex, also from the lungs of the fowl, and discussed the probability of its belonging to *Mesocestoides*, without, however, coming to a definite conclusion.

Quite recently (1926) Skrjabin and Schulz have stated their opinion that Alessandrini's view must be abandoned. These authors refer to *M. lineatus* a "*Dithyridium*" found by them in the abdominal cavity of the house-mouse and brown rat in Russia. The various suggestions referred to are all based on morphological considerations. Schwartz, however (1927), has obtained an adult *Mesocestoides* in dogs and cats fed experimentally with a "*Dithyridium*" from a mongoose.

It may be mentioned here that a "*Dithyridium*" (the *Cysticercus elongatus* of Blumberg, 1882, or *Dithyridium bailleti* of Railliet, 1885) has been recorded from the pleural and peritoneal cavities of the cat and dog.

ANOPLOCEPHALIDÆ.

In the family **Anoplocephalidæ** the scolex is unarmed and without a rostellum, and the suckers are also usually unarmed. The segments are usually numerous and considerably broader than long. The genital pores are marginal. There may be either one or two sets of reproductive organs in each segment, and either one genital pore, situated on one side, or a pore on each side. The testes are generally numerous. The uterus may be persistent or may be replaced by egg-capsules. In the former case it is transversely elongate and may be tubular, sac-like, branched or reticulate. The eggs usually have thin outer envelopes, and the embryo may be enclosed in an inner shell, or embryophore, of a peculiar form, drawn out on one side into a pair of horns, and known as a "pyriform apparatus."

The adult worms occur in mammals, birds and reptiles. Nothing appears to be known of the life-history of any member of the family, and it is still uncertain, even in the case of those common species which occur in sheep and other domestic animals, and are sometimes responsible for severe losses, whether there is an intermediate host or whether the life-history is direct.

In **Anoplocephala** E. Blanchard, 1848, the segments are generally very short and relatively broad. There is a single set of genital organs in each segment, and the genital pores are unilateral (*i.e.*, all on the same side of the strobila). The genital ducts cross the longitudinal excretory

vessels and nerve on the dorsal side, the vagina being ventral to the cirrus-sac. There is an external vesicula seminalis. The testes may be confined to the aporal side of the segment, or may extend fairly uniformly across it. The female glands are on the pore side of the median field. The uterus is a transversely elongate sac, with pocket-like extensions anteriorly and posteriorly. The eggs have a well-developed "pyriform apparatus." The adult worms occur in mammals and birds.

Anoplocephala perfoliata (Goeze, 1782) occurs in the large intestine of the horse, donkey, mule and zebra, and has a world-wide distribution. It may attain a length of 80 mm. and a maximum width of about 12 mm. The scolex is about 2 to 3 mm. in diameter, with the suckers opening anteriorly, and bears posteriorly four short, blunt lobes or lappets, two dorsally and two ventrally. The eggs measure 0.065 to 0.08 mm. in diameter.

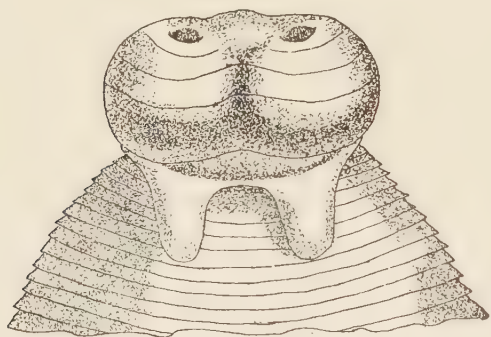


FIG. 49.—*Anoplocephala perfoliata*: SCOLEX.
(FROM NEUMANN, AFTER RAILLIET.)

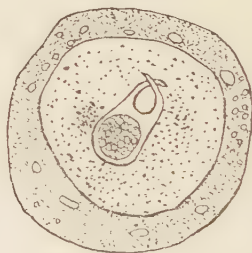


FIG. 50.—*Anoplocephala perfoliata*: EGG. (AFTER YORKE AND SOUTHWELL.)

Anoplocephala magna (Abildgaard, 1789) is a much larger form, measuring 9 to 80 cm. in length and up to 20 mm. in width. It differs from *A. perfoliata* in the absence of posterior lappets on the scolex. The scolex has a diameter of 4 to 6 mm. The eggs measure 0.05 to 0.06 mm. *A. plicata* (Zeder, 1800), and several varieties ascribed to it, are now regarded as synonyms of this species. *A. magna* occurs in the small intestine, and rarely in the stomach, of horses, donkeys, mules and zebras in Europe and Africa.

Anoplocephala mamillana (Mehlis, in Gurlt, 1831) is also a parasite of the small intestine, and rarely stomach, of the horse in Europe and Asia. This is a relatively small species, measuring 6 to 50 mm. in length and 4 to 6 mm. in maximum width. The scolex has a diameter of only about 0.7 mm., and the suckers are dorsally and ventrally placed, with openings in the form of longitudinal slits. The strobila consists of about

thirty to fifty segments. The eggs are ovoid and measure 0.088×0.05 to 0.066 mm. Baer has recently referred this species, among others, to the genus *Paranoplocephala* Lühe, 1910 (= *Anoplocephaloides* Baer, 1924), chiefly on the ground of differences observed in the arrangement of the excretory canals. These, in *A. mamillana*, are said to be simple and not to form a complex network as in the other species from horses just mentioned.

Anoplocephala minima Mello, 1912, from the fowl, is incompletely described, and probably does not belong to this genus. It may be mentioned here that Gaiger, in 1915, recorded the occurrence of a species of *Anoplocephala* in a dog.

In **Bertiella** Stiles and Hassall, 1912, there is a single set of reproductive organs in each segment, the genital pores are irregularly alternating, and the testes are dorsally and anteriorly situated, extending across the whole of the median field between the lateral excretory canals. The uterus is similar to that of *Anoplocephala*. The eggs may or may not be provided with a "pyriform apparatus." The adults occur in Primates.

B. studeri (= *satyri*) (R. Blanchard, 1891), whose normal hosts appear to be apes (orang-utan, chimpanzee, gibbon) and monkeys, has been recorded once from a child in Mauritius. It is a very variable form, measuring usually 200 to 300×7 to 15 mm., with very short segments. The eggs measure 0.045 to 0.06 mm. in diameter, and have a "pyriform apparatus" with long filaments.

In the genus **Aporina** Fuhrmann, 1902, genital pores may be altogether absent, or may be present only in young segments, in which case they are irregularly alternating. The cirrus-sac is poorly developed. The female glands are situated in the poral half of the segment, and surrounded by the numerous testes. The uterus is at first a transverse tube, subse-



FIG. 51.—*Anoplocephala mamillana*.
(FROM BAER, AFTER FUHRMANN.)

quently becoming sac-like and forming diverticula. The eggs are provided with two envelopes, but without a "pyriform apparatus." The adults occur in birds.

A. delafondi (Railliet, 1892) occurs in the domestic pigeon, wild rock-dove and other pigeons in Europe, Asia, Africa and America. It measures 70 to 140 mm. in length and 3 to 5 mm. in maximum width. The eggs are globular and have a diameter of 0.042 to 0.065 mm.

In the genus **Moniezia** Blanchard, 1891, there are two sets of genital organs in each segment. The segments are generally considerably broader than long. The genital ducts are dorsal to the longitudinal excretory canals. The vagina is ventral to the cirrus-sac on the right side, and dorsal to it on the left. At the junction of each segment with the next a series of "interproglottidal glands" is usually present dorsally



FIG. 52.—*Moniezia expansa* :
EGG. (ORIGINAL.)



FIG. 53.—*Moniezia expansa* : MATURE SEGMENT.
(PARTLY AFTER THEILER.)
i., interproglottidal glands.

and ventrally. The two uteri of each gravid segment are reticulate, and may become fused in the middle line. They may be confined to the median field or may extend laterally beyond, and dorsally to, the excretory canals and nerves. The eggs have a well-developed "pyriform apparatus," whose horns usually end in a cap or disc. The adult worms are parasitic in mammals.

A considerable number of species of *Moniezia* from domestic ruminants have been described as distinct, but Miss Theiler, in a recent revision of the genus, has shown that many of the supposed specific characters are due to individual variation, or are not constant throughout the whole strobila even of a single worm. She therefore considers that the species in question may probably be reduced to two, or at most three.

Moniezia expansa (Rudolphi, 1810) is a common and widely distributed species, occurring in the small intestine of the sheep, goat and ox,

besides a number of wild ruminants. It has a scolex measuring 0.36 to 0.8 mm. in diameter. The suckers are often very prominent, and have slit-like apertures. The segments are all wider than long. The total length of the strobila may be from 1 to 6 metres, and the maximum width attained is about 16 mm. The interproglottidal glands are saccular (*i.e.*, arranged round a series of blind sacs). The eggs measure 0.05 to 0.07 mm. in diameter.

Moniezia benedeni (Moniez, 1879) is a rather larger form with a similar host-range and distribution to *M. expansa*. The length of the strobila is from 1 to 4 metres or more, and the maximum width about 26 mm. The scolex measures from 0.8 mm. to more than 1 mm. in diameter. The interproglottidal glands are linear (*i.e.*, arranged in a transverse line in the median field). The eggs measure 0.08 to 0.085 mm. in diameter.

Moniezia denticulata (Rudolphi, 1810) (= *alba* Perroncito, 1878), occurring in sheep and cattle in Southern Europe and Northern Africa, is said to be entirely without interproglottidal glands. The scolex is

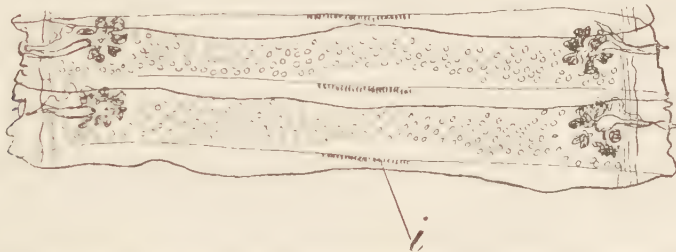


FIG. 54.—*Moniezia benedeni*: MATURE SEGMENTS. (PARTLY AFTER THEILER.)
i., interproglottidal glands.

very large (1.15 to 1.4 mm. in diameter). The strobila attains a length of 60 to 250 cm., and a width of 14 mm. The segments occasionally become longer than wide. The eggs measure 0.06 to 0.088 mm.

Moniezia pallida Monnig, 1926, has been described recently from the intestine of the horse in the Transvaal. Monnig states that he had seen fragments of this worm on three occasions among horse-parasites in South Africa before receiving complete specimens collected by Veglia. The maximum length, according to Monnig, is 138 cm., and the maximum width 21 mm. The diameter of the scolex is 0.75 mm. The segments are all much broader than long, and the interproglottidal glands are linear, but indistinct. The uterus extends laterally beyond the excretory canals dorsally, and sometimes also ventrally. In the last respect the species differs from all others.

The following two genera (*Avitellina* and *Stilesia*) possess certain peculiarities which justify their being placed in a special subfamily,

Avitellininae, within the family Anoplocephalidæ. In these forms there is a single set of reproductive organs in each segment, and the genital pores are irregularly alternating. A paruterine organ or organs are developed in connection with the uterus in the gravid segments. The genital ducts pass dorsally to the excretory canals or between them. The testes are arranged in groups near the lateral margins of the segments, and are absent from the median field. There is a single ovary, and the uterus is single or consists of two portions joined by an "interuterine duct." The most remarkable feature of the group is that a separate vitelline gland and shell-gland are absent, the nutritive function of the former being apparently undertaken by certain cells in the ovary and in the wall of the uterus. The eggs have two thin envelopes and are without a "pyriform apparatus." The adult worms occur in the intestine or bile-ducts of ruminants.

In the genus **Avitellina** Gough, 1911, the strobila is thin and narrow. The segments are broader than long, and are flattened in the anterior part of the strobila, becoming narrower and nearly cylindrical posteriorly. The genital ducts are dorsal to both excretory canals. The testes are typically in four sets in each segment, one on either side of each of the large longitudinal excretory canals. The ovary is on the side nearest to the pore. The uterus is single, and there is a single paruterine organ in each gravid segment.



FIG. 55.—*Avitellina centripunctata*: SCOLEX.
(AFTER GOUGH.)

There is some uncertainty as to the number of species of this genus occurring in sheep and other domesticated ruminants in different parts of the world. This arises mainly from the fact that the morphology of the European form, *A. centripunctata* (Rivolta, 1874) remained, until recently, very imperfectly described, and the only reasonably detailed description available (that of Gough, published in 1909 and 1911) of a form assumed to be *A. centripunctata* was based on South African material. Woodland has recently (1927) redescribed what is presumably Rivolta's species, on the basis of Italian material, and has thrown doubt upon the accuracy of Gough's determination of his South African specimens, besides describing three other forms from Africa and India which he considers to be distinct species. It seems therefore that either there is a multiplicity of species, or *A. centripunctata* is a very variable form.

For the present *A. centripunctata* must be regarded as a parasite of the sheep in Europe alone, and specimens from other parts of the world must be considered as doubtfully belonging to this species until their morphology has been carefully studied.

A. centripunctata (Rivolta) attains a length, probably, of 2 to 3 metres, and a width of some 2 mm. The worm has a gelatinous, semi-translucent appearance when fresh, with a median opaque line, bordered by two very transparent lines, due to the extremely wide ventral excretory

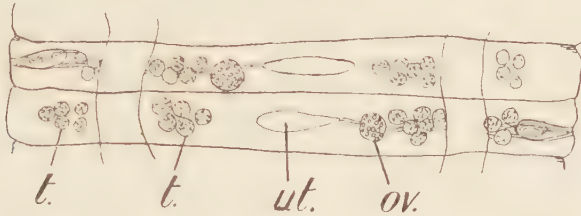


FIG. 56.—*Aritellina centripunctata*: MATURE SEGMENTS. (AFTER BAER.)

ov., ovary; t., t., testes; ut., uterus.

canals. The scolex is large (about 1.5 to 2 mm. in diameter), and the suckers are directed outwards and forwards. In mature segments all the genital organs lie in one transverse plane. The testes lie in four columns, those external to the ventral canals being, according to Woodland, about two testes deep transversely, while those on the median side of the canals are about four testes deep. The cirrus-sac measures 0.117 to 0.146 mm. long and 0.044 to 0.073 mm. wide, apparently increasing in length and decreasing in width in the older segments. The vagina is posterior to the cirrus-sac, and usually dorsal to it on the left side of the strobila, and ventral on the right.

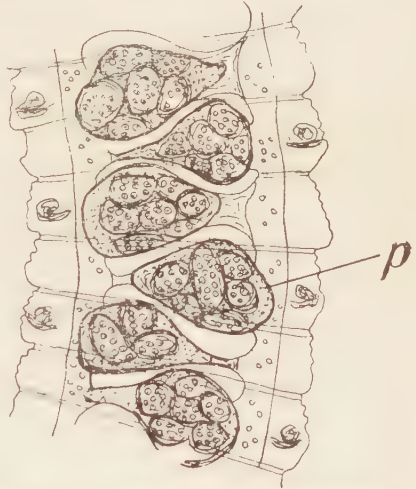


FIG. 57.—*Aritellina centripunctata*: GRAVID SEGMENTS. (AFTER WOODLAND, MODIFIED.)

p., paruterine organ.

The paruterine organs, at first forming a single median longitudinal row of oval sacs, finally become pear-shaped structures alternating from side to side, with their long axes arranged transversely. By the growth of fibrous tissue within them their cavities become subdivided into a number of capsules containing eggs. Woodland finds that the paruterine organs ultimately open into the ventral excretory canals, into which the egg-capsules are discharged. The excretory canals thus appear to function as ducts conveying the eggs to the exterior. The outer envelope of the eggs, according to Wood-

land's measurements, is about 0.022 mm. in diameter, the inner envelope 0.018 mm., and the embryo 0.0146 mm.

To what extent the differences between Woodland's and Gough's descriptions are to be ascribed to real differences in the material or to differences in interpretation, or in state of preservation, it is at present impossible to say. Woodland is inclined to regard Gough's South African form as a distinct species, and suggests for it the name *A. goughi*. Altogether Woodland recognizes five species of *Avitellina*, to which he gives the following key, which is here quoted in his own words:

1. Mature paruterine organs lie in a single row in the median axis of the strobila and individually do not occupy more than one proglottid antero-posteriorly. Outer column of testes one-testis deep and kidney-shaped paruterine organs *A. sudanea*.
Mature paruterine organs alternate from side to side of the middle line and individually occupy to a greater or less extent more than one proglottid longitudinally (2)
2. Outer columns of testes one-testis deep and immature paruterine organs snail-shaped *A. lahorea*.
Outer columns of testes two- to three-testes deep (3)
3. Mature paruterine organs pear-shaped in surface view and vertical and non-overlapping in sagittal section *A. centripunctata*.
Mature paruterine organs pear-shaped and oblique and overlapping in sagittal section, and with anterior annular thickening on each proglottid and anterior genital apertures situated on the thickening *A. chalmersi*.
Mature paruterine organs resemble bunches of bananas in surface view, the eggs being lodged in longitudinally disposed pockets, each the length of the organ *A. goughi*.

The hosts and localities of Woodland's new species (all of which are based on fragments of strobila) are as follows. *A. sudanea* and *A. chalmersi* both came from sheep in the Sudan. *A. lahorea* was found in a bottle containing also *Dipylidium* sp. from a dog, and is assumed to have been placed there accidentally, and to have come from a sheep, goat or other ruminant of Indian origin. As regards *A. goughi*, its hosts appear to include the sheep, goat, ox, buffalo and a number of African antelopes.

A. laciniosa Blei, 1922, and *Hexastichorchis pintneri* Blei, 1922, both found in sheep in the Ukraine, are regarded by Baer, who has examined the original material, as synonyms of *A. centripunctata*. The genus *Hexastichorchis* Blei was based on the presence of six, instead of four, sets of testes, situated between and on either side of the four longitudinal

excretory canals. Baer states that this is a not uncommon abnormality in *A. centripunctata*, and may occur in portions of strobilæ of which the rest shows the usual arrangement.

Stilesia Railliet, 1893, differs from *Aritellina* chiefly in the following characters: The genital ducts pass between the dorsal and ventral longitudinal excretory canals; the testes in each mature segment are arranged

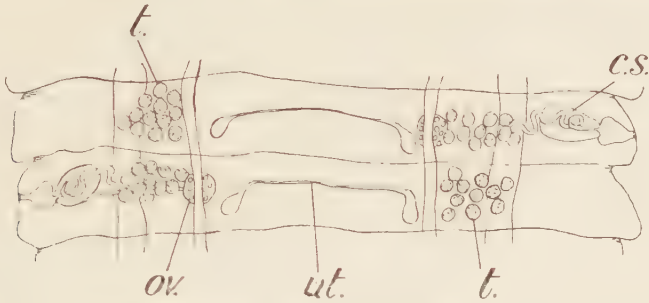


FIG. 58.—*Stilesia hepatica* : MATURE SEGMENTS. (AFTER BAER.)
c.s., cirrus-sac; ov., ovary; t., t., testes; ut., uterus.

in two lateral sets only; the uterus consists of two portions, and there are two paruterine organs in each gravid segment.

Stilesia hepatica Wölfhügel, 1903, occurs in the bile-ducts of the sheep, goat and various wild ruminants, chiefly in Africa. The strobila is thin, gelatinous and semi-translucent when fresh. It is very difficult to obtain complete specimens. According to Gough, the length of such

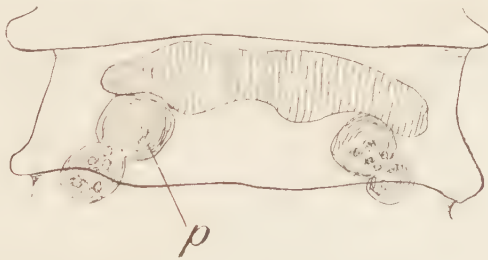


FIG. 59.—*Stilesia hepatica* : GRAVID SEGMENT. (AFTER BAER.)
p., paruterine organ.

a specimen would probably be between 20 cm. and 50 cm. The suckers are outwardly and forwardly directed. The scolex is often followed by a contracted and swollen portion, apparently serving as a "holdfast." There are from ten to twelve testes on each side of the segment, arranged mainly on the median side of, or dorsal to, the ventral excretory canal. The two portions of the uterus are connected by an "interuterine duct." The outer shell of the eggs is ovoid, measuring 0.026 × 0.016 to 0.019 mm.

S. globipunctata (Rivolta, 1874) occurs in the small intestine of the sheep and goat in Europe and India. The scolex has a diameter of 0.7 to 0.9 mm. The length of the strobila is 45 to 60 cm., and its maximum width 2.5 mm. The anterior portion of the strobila is sometimes contracted, as in *S. hepatica*. The segments are all broader than long, but become relatively longer posteriorly. There are from four to seven testes on each side of the segment, all situated laterally to the ventral canal and between it and the nerve. The vas deferens forms only three or four loose coils between the nerve and the ventral canal. The vagina is dorsal to the cirrus-sac and to the ventral canal, after crossing which it expands to form a receptaculum seminis. One portion of the double uterus lies dorsally to the ovary, the other near the ventral canal of the other side. The outer envelope of the eggs measures 0.056×0.027 mm.

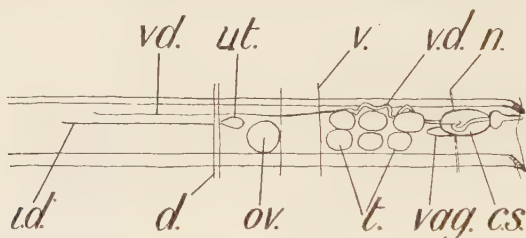


FIG. 60.—*Stilesia globipunctata*: RIGHT HALF OF A MATURE SEGMENT.
(AFTER GOUGH.)

c.s., cirrus-sac; *d.*, dorsal vessel; *i.d.*, interuterine duct; *n.*, nerve; *ov.*, ovary; *t.*, testes;
ut., uterus; *v.*, ventral canal; *vag.*, vagina; *v.d.*, vas deferens.

S. vittata Railliet, 1896, from the small intestine of the camel in India and North Africa, is very similar to the last species, from which it differs chiefly in the arrangement of the vas deferens, which here forms a dense mass of coils between the nerve and the ventral canal, serving as a vesicula seminalis.

The genus ***Thysanosoma*** Diesing, 1835, differs so considerably from other Anoplocephalidæ that it is placed by some authors in a special subfamily, ***Thysanosominæ***. In this genus there is a double set of reproductive organs in each segment, but only a single, transversely elongate uterus. This is composed of several or numerous intercommunicating sacs or pouches, each with a paruterine organ into which the eggs probably pass eventually. The genital pores may be paired in each segment or may be irregularly alternating. In the latter case the cirrus-sac, vagina and ovary of one side are absent. The genital ducts pass between the dorsal and ventral excretory canals. The "pyriform apparatus" of the eggs is without horns. The adults occur in the intestine of mammals.

Thysanosoma actinioides Diesing, 1835, occurs in sheep, cattle and various deer in North and South America. It is said to be very common in sheep in the plains of the Western United States, where it appears to be responsible at times for considerable losses. This species measures 15 to 30 cm. in length, with a maximum width of 8 mm. The scolex is from 1 to 1.5 mm. in diameter. The segments are much broader than long, and are remarkable for the possession of long fringes on their posterior margins. There are two genital pores and two sets of reproductive organs in each segment. The testes occupy the median field.

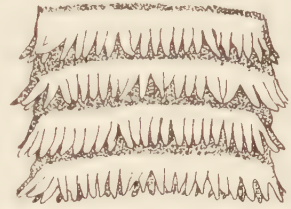


FIG. 61.—*Thysanosoma actinioides*: FOUR SEGMENTS. (FROM NEUMANN, AFTER RAILLIET.)

Helictometra giardi (Moniez, 1879) occurs in sheep, and possibly in cattle, in Europe, and has also been recorded from Africa and America. There is a single record of its occurrence in a pig, but this may be taken to have been an accidental infection. The worm attains a length of 2 metres or more, and a maximum width of about 10 mm. The scolex may be more than 1 mm. in diameter. The segments are very short, and without fringes. The genital pores are usually irregularly alternating, and there is usually only a single set of genital organs in each segment, though occasionally

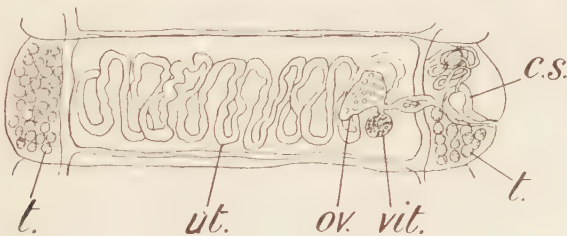


FIG. 62.—*Helictometra giardi*: MATURE SEGMENT. (AFTER BAER.)

c.s., cirrus-sac; ov., ovary; t., t., testes; ut., uterus; vit., vitellarium.

there are two sets. The testes are in the lateral fields, between the excretory canals and the lateral margins. The uterus is an undulating tube occupying the greater part of the segment. The eggs have a diameter of 0.016 to 0.027 mm.

This species, formerly referred to *Thysanosoma*, has been placed in a new genus, *Helictometra*, by Baer (1927), on account of the arrangement of the testes, the presence of numerous paruterine organs and the presence of rudimentary vitelline and shell glands.

DAVAINEIDÆ.

In the family **Davaineidæ** the scolex has a retractile rostellum armed with one or more crowns of small but very numerous hammer-shaped or T-shaped hooks. The suckers also, in many species, bear numerous minute hooks or spines arranged in concentric circles. In some, however, they are unarmed. Each segment may contain a single or a double set of genital organs. In the latter case there are two genital pores to each segment. When only one set of organs is present, the pores may be either unilateral (all on the same side of the strobila) or regularly or irregularly alternating. There may or may not be a persistent uterus in

the gravid segments. When persistent, the uterus is sac-like. When temporary, it may be sac-like or branched, and is replaced later either by numerous "egg-capsules" (masses of thickened parenchyme enclosing one or several eggs) or by a single large capsule following on the formation of a "paruterine organ." The embryos are enclosed in thin membranous envelopes, a hard egg-shell being absent.

The adult worms of this family occur in the intestine of mammals and birds. The life-history is known in but few cases. Where known, the intermediate host is usually an invertebrate (mollusc or insect).

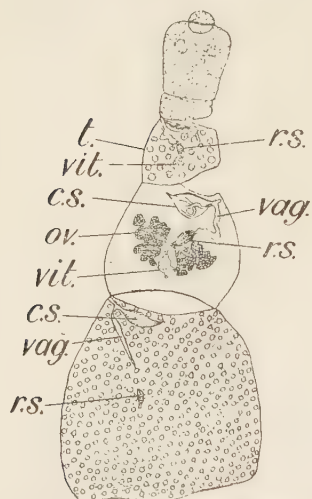


FIG. 63.—*Davainea proglottina*: ENTIRE WORM. (AFTER BLANCHARD.)

c.s., cirrus-sac; ov., ovary; r.s., receptaculum seminis; t., testes; vag., vagina; vit., vitellarium.

The genus **Davainea** Blanchard, 1891, as now restricted, contains only one species parasitic in a domestic host. This is **D. proglottina** (Davaine, 1860), which occurs in the fowl and is of cosmopolitan distribution. In

this form the strobila is short, consisting of only four to nine segments. It measures 0.5 to 3 mm. in length and 0.18 to 0.6 mm. in maximum width. The musculature is feebly developed. The rostellum bears sixty to ninety-five hooks, 0.005 to 0.008 mm. long. The suckers are armed with several rows of hooks, which are easily shed. The genital pores are regularly alternating, and are situated at the anterior corners of the segments. The cirrus-sac is large, extending across about two-thirds of the width of the segment. The testes are relatively few (twelve to fifteen), arranged in two rows at the back of the segment. In gravid segments the eggs are distributed singly in the parenchyme.

The intermediate hosts of this species are slugs (*Agriolimax agrestis*, *Limax cinereus*, *L. variegatus*, *L. flavus*).

The most important genus of this family is **Raillietina** Fuhrmann, 1920, which contains a very large number of species separated by Fuhrmann from the genus *Davainea* as formerly understood.*

In *Raillietina* the segments are numerous, and the genital pores may be unilateral or irregularly alternating. The suckers may be unarmed or may bear hooks or spines, which are often very readily shed, and therefore are not present in every specimen. The egg-capsules may contain one or

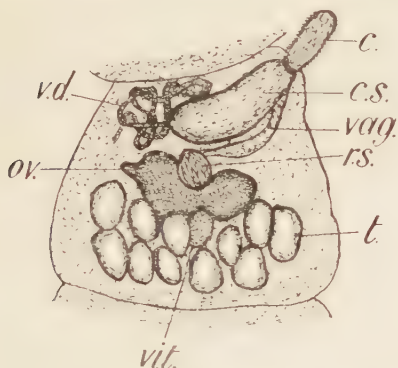


FIG. 64.—*Davainea proglottina*: MATURE SEGMENT. (AFTER MEGGITT.)

c., cirrus; c.s., cirrus-sac; ov., ovary; r.s., receptaculum seminis; t., testes; vag., vagina; v.d., vas deferens; vit., vitellarium.

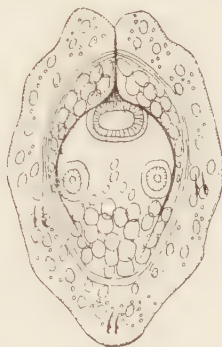


FIG. 65.—*Davainea proglottina*: CYSTICERCOID. (FROM STILES, AFTER GRASSI AND ROVELLI.)

several eggs. By far the greater number of species occur as adults in birds, though a few are parasitic in mammals, and of these three reputed species have been recorded from man. The intermediate hosts, when known, are usually insects.

This genus has been divided into subgenera, for the separation of which the following key may be given:

A. Genital pores unilateral:

- (1) Egg-capsules each containing several eggs. *Raillietina* (= *Ransomia* Fuhrmann, 1920).
- (2) Egg-capsules each containing one egg. *Paroniella* Fuhrm., 1920.

B. Genital pores irregularly alternating:

- (1) Egg-capsules each containing several eggs. *Fuhrmannetta* Stiles and Orleman, 1926.
- (2) Egg-capsules each containing one egg. *Skrjabinia* Fuhrm., 1920.

* The classification adopted by this author is admittedly somewhat artificial, and its chief recommendation is the convenience of splitting up into smaller groups the species formerly contained in the very large and unwieldy genus *Davainea*.

The following three species all appear to belong to the subgenus *Raillietina*. **R. (R.) madagascariensis** (Davaine, 1870) (synonym, *demerariensis* Daniels, 1895) has been recorded as a human parasite on several occasions, usually in children, in the following localities: Mayotte, Nossi-Bé (islands near Madagascar), Mauritius, Bangkok (Siam), Georgetown (British Guiana) and the Philippines. It is described as having a



FIG. 66.—*Raillietina echinobothrida*. (AFTER MEGGITT.)
A, scolex; B, hook from rostellum.

length of about 25 cm. and possessing 600 to 700 segments. The scolex is about 1 mm. in diameter, and the rostellum is stout, with a double crown of about ninety hooks, 0.018 mm. long. The suckers are large and probably armed with spines. In the anterior portion of the strobila the segments are wider than long, but the gravid segments are longer than wide (2×1.4 mm.). The genital pores are unilateral and situated near

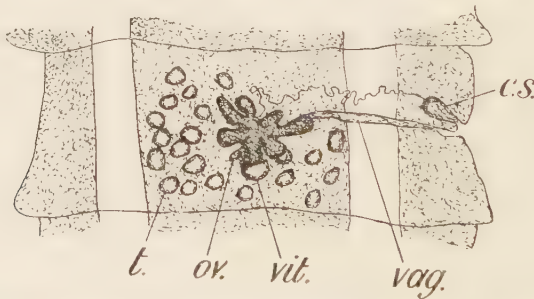


FIG. 67.—*Raillietina echinobothrida*: MATURE SEGMENT. (AFTER MEGGITT.)
c.s., cirrus-sac; ov., ovary; t., testes; vag., vagina; vit., vitellarium.

the anterior end of the segment. The egg-capsules contain 300 to 400 eggs. The embryos have a maximum diameter of 0.008 to 0.015 mm. The intermediate host of this species is not known, but cockroaches are suspected of harbouring it.

***Raillietina* (R.) asiatica** (v. Linstow, 1901) is known only from a single specimen, of which the scolex was missing, recorded from man in Russian

Turkestan. The length of the specimen was 298 mm., and its maximum width 1.17 mm. All the segments were broader than long.

Raillietina (R.) formosana Akashi, 1916, is known from a single occurrence in the faeces of a child in Formosa. It is described as having a length of 43 cm. The scolex is 0.4 mm. in diameter, and the rostellum bears a double row of numerous hooks. The suckers are said to be unarmed, 0.12 mm. in diameter. The segments attain a great length in the posterior quarter of the strobila (20 to 25 mm. long by 1 mm. wide). The genital pores are unilateral and situated near the anterior end of the segment. The eggs measure 0.099×0.046 mm.

The number of species of *Raillietina* occurring in domesticated birds is so large, and their characters for the most part so similar, that it is not practicable to give here a separate specific description of each of them. Table II (p. 94) summarizes some of their more readily observed characters, and will, it is hoped, be helpful in distinguishing them. In addition to those referred to in the table, some six species have been described from guinea-fowl. These, however, occur in the birds in their wild state in Africa, and it is doubtful whether any of them are likely to be met with in the domesticated variety. Similarly, about eleven species of *Raillietina* are known to occur in birds of the pigeon tribe, but of these probably only the three mentioned in the table need be considered here as parasites of the domestic pigeon.

As regards the life-history of the species of *Raillietina* parasitic in birds, the cysticeroid of *R. echinobothrida*, according to Piana, occurs in snails (*Helix carthusianella* and *H. maculosa*). Grassi and Rovelli, however, did not succeed in confirming this observation. According to Ackert, the intermediate host of both *R. tetragona* and *R. cesticillus* is the house-fly. Joyeux, however, has recorded the negative results of attempts to infect this insect with *R. cesticillus*.

The genus **Davainoides** Fuhrmann, 1920, differs from *Raillietina* in having from six to twenty longitudinal excretory vessels instead of the usual two pairs. The genital pores are irregularly alternating, the testes numerous, and the eggs are enclosed singly in capsules. The genus

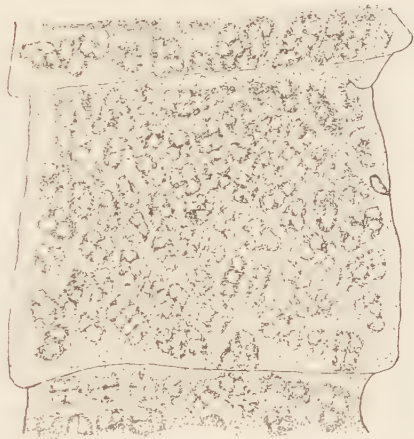


FIG. 68. *Raillietina tetragona*: GRAVID SEGMENT. (FROM STILES, AFTER KRABBE.)

TABLE II.—SPECIES OF *RAILLIETINA* OCCURRING IN DOMESTIC BIRDS.

Species.	Length in Mm.	Width in Mm.	Approximate Number of Rostellar Hooks.	Length in μ of Rostellar Hooks.	Acetabular Hooks.	Genital Pores.	Extent of Cirrus-Sac.	Number of Eggs per Capsule.	Diameter in μ of Eggs.	Known Geographical Distribution.	Domestic Hosts.
<i>tetragona</i> (Molin, 1858)	Up to 250	1 to 4	100	6 to 9	8 to 10 rows	Unilateral	Not reaching ventral excretory canal	6 to 12	25 to 50	Cosmopolitan	Fowl, guinea-fowl, pea-fowl.
<i>echinobothrida</i> (Méglin, 1880)	250	1 to 4	200	10 to 13	8 to 10 rows	Alternating	Not reaching ventral excretory canal	6 to 12	25 to 50	Cosmopolitan	Fowl.
<i>mutabilis</i> (Rüther, 1901)	0.9 to 2	0.42 to 0.45	160	27	Absent	Alternating	—	2 to 3	10 to 20	Cosmopolitan	Fowl.
<i>volzii</i> (Fuhrmann, 1905)	40 to 60	2	240	10	Present	Unilateral	Reaching excretory canal	30	8 to 12	Sumatra	Fowl.
<i>colni</i> (Baczynska, 1914)	20 to 30	1.7	160	8	14 rows	Unilateral	Not reaching excretory canal	10 to 15	Several	W. Africa	Fowl.
<i>penetrans</i> (Baczynska, 1914)	30 to 40	1.5	240	13	14 to 15 rows	Unilateral	—	15 to 20	Several	W. Africa	Fowl.
<i>grabbeii</i> Böhm, 1925	170 to 440	—	200	10 and 13	Present	Unilateral	Not reaching excretory canal	24 to 32	Up to 6	Austria	Fowl.
<i>birmanica</i> Meggitt, 1926	8 to 10	1 to 2	300	10 and 12	Absent	Alternating	Extending beyond excretory canal	20 to 25	Several	Burma	Fowl.
<i>pseudoechinobothrida</i> Meggitt, 1926	80 to 90	1 to 8 [? 1.8]	300	8 to 13	Present	Alternating	Not reaching excretory canal	30 to 50	3 to 4	Burma	Fowl.
<i>parvuncinata</i> Meggitt and Po Saw, 1924	110 to 120	0.2	150	7 to 9	9 rows	Unilateral	Reaching nerve	24 to 39	5 to 13	Burma	Duck.
<i>crassula</i> (Rud., 1819) Fuhrm.	250 to 400	4	70	20	Present	Alternating	0.1 mm. long	30 to 40	3 to 4	Europe, Africa, S. America	Pigeon.
<i>clerci</i> * Fuhrm., 1920 (= <i>crassula</i> of Clerc, 1906)	Up to 212	1.5	180 (Joyeux) 400 (Clerc)	8 to 10	5 or 6 rows	Unilateral	Not reaching excretory canal	24 to 28	6 to 8	Asia, Africa	Pigeon.
<i>nagpurensis</i> Moghe, 1925	250 to 274	1.9	220	19 and 17	A single row	Unilateral	Not reaching excretory canal	19 to 22	3 to 8	India	Pigeon.
<i>cestitillus</i> (Molin, 1858)	Up to 130	1.5 to 3	[200] or 400 to 500	7 to 12	Absent	Alternating	Reaching excretory canal	20 to 30	1	Cosmopolitan	Fowl, guinea-fowl, turkey.
<i>microcotyle</i> (Skrjabin, 1914)	22	1.5	—	—	—	Alternating	0.13 to 0.14 mm. long	30	1 [Embryo 40]	Italy	Duck.
<i>columbae</i> † (Fuhrmann, 1909)	60 to 70	1	120	11	—	Alternating	Extending well beyond ventral excretory canal	30	1 [Embryo 36]	Europe	Pigeon.
<i>anatina</i> ‡ (Fuhrmann, 1909)	15	1	300	14 to 16	—	Alternating	—	—	—	Italy, India	Duck.

Subgenus *Raillietina* and *Fuhrmannella*.Subgenus *Skrjabinia*.

* Characters taken mainly from a description by Joyeux, 1923.

† This species is normally a parasite of the wood-pigeon, but has been met with by the writer in the domestic pigeon in England.

‡ Known only from immature specimens.

contains a form—**D. vigintivasus** (Skrjabin, 1914)—found in the fowl in Brazil. This worm is about 250 to 300 mm. long, with a maximum width of 6 mm., and has ten dorsal and ten ventral excretory canals. The scolex is undescribed. There are more than 150 testes in each mature segment. These lie chiefly laterally and posteriorly to the female glands, which are median. The cirrus-sac is muscular and measures 0.68 mm. long and 0.25 mm. wide. The onchospheres are 0.055 mm. in diameter.

In **Cotugnia** Diamare, 1893, the scolex is large, and the rostellum has a swollen base and bears two alternating crowns of hooks having a thick, short blade, a thin "ventral" root and no "dorsal" root. The segments are broader than long, and contain a double set of genital organs, situated close to the longitudinal excretory canals on either side. The testes are numerous and generally posteriorly situated, extending laterally beyond the excretory canals. The eggs are ultimately enclosed singly in capsules. The adults occur in birds.

Cotugnia digonopora (Pasquale, 1890) occurs in the fowl in Eastern Europe, Asia and Africa. This species is 22 to 107 mm. in length and



FIG. 69.—*Cotugnia digonopora*: MATURE SEGMENT. (AFTER MEGGITT.)

c., cirrus; c.s., cirrus-sac; ov., ovary; t., testes; vag., vagina; v.d., vas deferens; vit., vitellarium.

1 to 4 mm. in maximum width. The rostellar hooks measure 0.008 to 0.012 mm. in length. There are about 100 testes in each mature segment. The eggs measure 0.063×0.058 mm.

Cotugnia fastigata Meggitt, 1920, is recorded from the domestic duck at Rangoon, Burma. In this form the strobila is 30 mm. long and 6 mm. wide (maximum). The scolex has a diameter of 0.5 to 0.6 mm. There are 200 rostellar hooks, measuring 0.02 mm. in length. The dorsal longitudinal excretory canals are absent in mature segments. The testes are arranged in a narrow band of two or three rows along the posterior border of the segment. The vagina is posterior to the cirrus-sac, and expands to form a receptaculum seminis. The ovaries are deeply lobed. A uterus

is present at first as a narrow, branched tube in front of the ovary, but soon disappears, the eggs then being enclosed singly in capsules.

C. cuneata Meggitt, 1924, is found in the pigeon in Burma and India. Meggitt has distinguished two varieties within the species. In the variety *tenuis* the strobila is 30 mm. long and up to 1 mm. in width. The scolex is 0.26 mm. in diameter, and the rostellum bears about 400 hooks, those of the two rows being respectively 0.014 and 0.018 mm. long. The cushion-like swelling at the base of the rostellum is covered with spines. The suckers are unarmed. The posterior segments are longer than broad. The musculature of the strobila is weak, and includes only two layers of longitudinal fibres. All the genital organs lie posteriorly to the genital pores. The testes are numerous, and extend forward between the ovaries to the level of the genital pores. The egg-capsules, in gravid segments, extend laterally beyond the excretory canals.

The variety *nervosa* agrees with the foregoing description in most respects, but differs in its much larger size (60×3 mm.), in having all the segments wider than long, and in possessing more powerful musculature, with three layers of longitudinal fibres.

In **Houttuynia** Fuhrmann, 1920, the rostellum bears, in addition to two alternating crowns of hooks, several series of small spines posteriorly. The strobila is relatively broad, and the genital pores are unilateral.

H. torquata Meggitt, 1924, occurs in the pigeon in Burma. This is a species attaining a length of 230 mm. and a width of 2.5 mm. The scolex is 0.09 to 0.095 mm. in diameter. There are 150 rostellar hooks, those of the two rows measuring 0.007 and 0.0075 mm. respectively. The base of the rostellum forms a barrel-shaped swelling covered with minute spines. The suckers are armed with about five rows of thorn-shaped hooks. There are from eight to ten testes in each mature segment, of which two are situated on the pore side, one behind the female organs and the rest on the aporal side. The cirrus-sac is small and contains a small internal seminal vesicle. The ovary is bilobed, each lobe being much subdivided. The uterus is temporary, and the eggs eventually become enclosed in groups of three to five in capsules, of which there are thirty to forty in each segment.

DILEPIDIDÆ.

In the family **Dilepididæ** a rostellum is usually, though not invariably, present. It may be armed with one, two or several crowns of hooks, or unarmed. The suckers are unarmed. The segments may contain a single or a double set of genital organs, and the genital pores may be paired or single, and in the latter case unilateral or regularly or irregularly

alternating. The testes are numerous and usually situated behind the female organs. There is typically a persistent uterus, but this organ is sometimes replaced by egg-capsules. In certain genera (subfamily Paruterininae) a special paruterine organ is developed, or several such organs, into which the eggs ultimately pass. The adult worms occur in members of all the groups of vertebrates.

In the genus *Amœbotænia* Cohn, 1899, the rostellum carries a single crown of hooks. The segments are relatively few, and are broader than long. The genital pores are regularly alternating. There are twelve or more testes, situated posteriorly. The uterus is persistent and sac-like. The adults occur in birds and mammals. *Amœbotænia sphenoides* (Railliet, 1892) is a parasite of the fowl, occurring in Europe, Asia, Australia and South America. It is a small species, usually 2 to 4 mm. in length and not more than 1 mm. in width. The scolex is 0.16 to 0.2 mm.

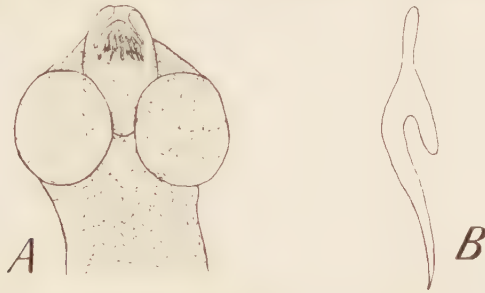


FIG. 70.—*Amœbotænia sphenoides*. (AFTER MEGGITT.)

A, scolex; B, hook from rostellum.

in diameter, and the rostellum 0.037 to 0.039 mm. There are twelve or fourteen hooks, 0.025 mm. in length. The strobila contains not more than twenty-four segments. The mature segments contain each twelve to fourteen testes. The uterus is lobed posteriorly. The eggs measure 0.035 to 0.042 mm. in diameter. The intermediate hosts are earthworms (species of *Allolobophora*, *Pheretima* and *Oncerodrilus*).

In *Choanotænia* Railliet, 1896, the rostellum bears a single crown of hooks. The genital pores are irregularly alternating, the testes numerous and posterior, and the uterus sac-like. The adults are parasitic in birds and mammals.

Choanotænia infundibulum (Bloch, 1779) is a common parasite of the fowl and of other Galliform birds, and enjoys a world-wide distribution. It attains a length of 50 to 200 mm. The scolex is 0.4 mm. in diameter, and the rostellum 0.06 to 0.07 mm. The latter bears sixteen to twenty hooks, 0.025 to 0.03 mm. in length. The genital pores are

situated near the anterior end of the segments, and the cirrus-sac is small, not reaching the excretory canals. Each mature segment contains from twenty-five to sixty testes. The uterus is much subdivided, and resembles a mass of egg-capsules. The eggs measure 0.04 to 0.05×0.032 to

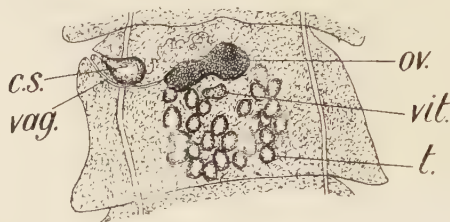


FIG. 71.—*Choanotenia infundibulum*: MATURE SEGMENT. (AFTER MEGGITT.)

c.s., cirrus-sac; ov., ovary; t., testes; vag., vagina; vit., vitellarium.

0.036 mm. The usual intermediate host appears to be the house-fly (*Musca domestica*). Joyeux has also succeeded in infecting experimentally a dung-beetle (*Geotrupes sylvaticus*).

In *Southwellia* Moghe, 1925, the rostellum has a double crown of hooks. The genital pores are unilateral. The testes are small, numerous and situated laterally and anteriorly to the ovary. The eggs become enclosed in capsules. *S. gallinarum* (Southwell, 1921) is found in the fowl in India. It measures 21 mm. in length and 2.5 mm. in maximum width. The scolex has a diameter of 0.5 mm., and there are 120 rostellar hooks, measuring 0.09 mm. in length. The segments are broader than long. The cirrus-sac is large and muscular. Mature segments contain thirty testes. The eggs are 0.035 mm. in diameter.

The most important genus of this family, from the veterinary and medical point of view, is *Dipylidium* Leuckart, 1863. In this genus the scolex is usually somewhat cylindrical in shape, and is armed with numerous hooks which have the appearance of being arranged in several transverse crowns, extending back for some distance from the apex. The hooks are of a characteristic rose-thorn shape, with an expanded, discoidal base instead of the more usual dorsal and ventral roots. Each segment contains a double set of genital organs, and two genital pores, situated opposite to each other on the lateral margins. The vagina opens behind the cirrus-sac. The testes are numerous, and are usually scattered throughout the whole extent of the medullary parenchyme. The female glands are placed near the longitudinal excretory canals of each side. The uterus is at first a reticulate structure, but later breaks down to form a number of rather thick-walled egg-capsules, each of which contains several eggs.

The adult worms occur in carnivorous mammals. The cysticeroids, which are of the "Cryptocystis" type, occur, so far as is known, in the body-cavity of fleas and lice which are ectoparasitic upon the final hosts. Thus the larval form of *D. caninum* occurs in the fleas (*Ctenocephalus canis*) of cats and dogs, and in the lice (*Trichodectes canis*) also found on these animals. It has also been recorded as occurring in the common human flea, *Pulex irritans*. Joyeux has shown that fleas become infected during their larval period, when their mouth-parts permit of the swallowing of the eggs of the worm. The hexacanth embryo burrows through the wall of the hinder part of the insect's gut and so reaches the body-cavity, where it develops into the cysticeroid. Reinfection of the final host readily takes place by the swallowing of these ectoparasites while licking itself. This species (*D. caninum*) has also occurred occasionally in



FIG. 72.—*Dipylidium caninum*: ROSTELLUM. (ORIGINAL.)

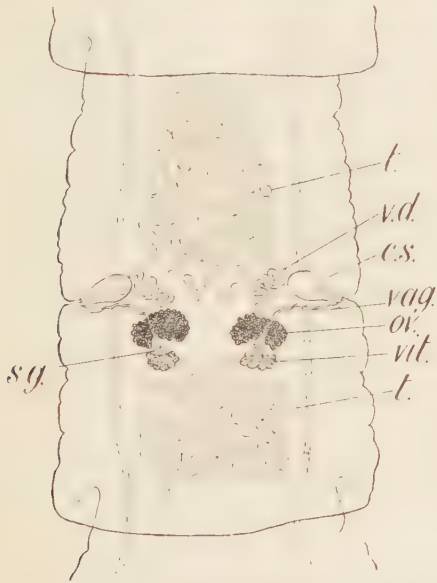


FIG. 73.—*Dipylidium caninum*: MATURE SEGMENT. (ORIGINAL.)

c.s., cirrus-sac; ov., ovary; s.g., shell-gland; t., t., testes; vag., vagina; v.d., vas deferens; vit., vitellarium.

man, doubtless as the result of the accidental ingestion of fleas, probably derived from dogs or cats.

This genus contains a considerable number of reputed species, found more especially in the dog and cat, of which animals they are often troublesome parasites, causing much digestive trouble, emaciation and weakness. The various forms recorded from these domestic animals cannot be individually described here, but some of their characters are tabulated below. In the writer's view it is improbable that all these forms can be maintained as distinct species, and many of them may represent nothing more than individual or local variations within a much smaller number of genuine species.

In size and other characters the common form, *D. caninum*, is extremely variable, while one factor that has probably had a good deal of influence upon the number of supposed species is the difficulty of counting accurately

the rows of hooks on the rostellum. The hooks are usually described in terms of transverse rows. They are not, however, arranged in straight



FIG. 74.—*Dipylidium sexcoronatum*: ROSTELLUM. (AFTER HALL.)

transverse rows, but appear rather to be in alternating *longitudinal* rows having a tendency to run spirally round the rostellum. It is possible for different observers, or the same observer, to obtain varying results when attempting to count the "transverse" rows in the same specimen. Still more is this the case with different specimens showing even the slightest individual variation either in the size and shape of the rostellum or in the total number of hooks. In the example of

D. caninum figured, for instance (Fig. 72), it would be possible to count six more or less straight transverse rows of which the individual hooks alternate, or, if the rows be regarded as wavy, either four or five rows.

The genus *Joyeuxia* Lopez-Neyra, 1927, has been erected to contain certain forms which differ from the typical species of *Dipylidium* in having a larger number of crowns of hooks (though these are of similar rose-thorn shape), a smaller number of testes, and relatively thin-walled egg-capsules containing each a single egg.

The genus *Diplopylidium* Beddard, 1913 (= *Progynopylidium* Skrjabin, 1924), as revised by Lopez-Neyra, differs from the preceding genera in



FIG. 75.—*Diplopylidium trinchessii*: HOOKS FROM ROSTELLUM. (AFTER DIAMARE.)

a, from first row; *b*, from second; *c*, from third; *d*, from fourth row.

having hooks with well-developed anterior and posterior roots of a more usual Tænioid form, instead of the peculiar discoidal base. The hooks are large in the anterior rows, decreasing in size posteriorly. The testes are relatively few, and the vagina runs below the cirrus-sac and opens in front of it or ventrally to it. The egg-capsules in gravid segments are without special cellular walls, and each contains a single egg.

DILEPIDIDÆ

101

Species.	Length of Strobila in Cm.	Maximum Width of Strobila in Mm.	Number of Crowns of Hooks on Strobilum.	Length of Hooks in μ .	Approximate Number of Testes in each Mature Segment.	Extent of Cirrus-Sacs.	Eggs in each Egg- capsule.	Domesti- cated Hosts of Adult Form.	Known Geo- graphical Distribution.
<i>Diplopidium</i> : <i>caninum</i> (1758)	15 to 50	2 to 3	3 to 4	Anteriorly 12 to 15, posteriorly 5 to 7.	100 to 200	Usually not reaching lateral excretory canals	4 to 20	Dog, cat; Cosmo- politan.	
<i>oerleyi</i> v. Rátz, 1900	5 to 11	2	5	—	90 to 100	Beyond excretory canals	Several	Cat	Hungary.
<i>sexocoronatum</i> v. Rátz, 1900	10 to 30	2	6 [- 7]	Anteriorly 11, posteriorly 4.	130 to 175	As far as, but not be- yond, excretory canals	2 to 15	Dog, cat	E u r o p e, India, N. America.
<i>walkeri</i> Sondhi, 1923	10 to 28	2.5	6 to 7	Anteriorly 12, posteriorly 2.	225	Nearly or quite reaching excretory canals	1 to 15	Dog	India.
<i>rossicum</i> Skrjabin, 1922	16.8	1.06	6 to 7	Anteriorly 15, posteriorly 12.5.	131	A little beyond excre- tory canals	Several	Dog	Russia.
<i>gracile</i> Millzner, 1926	20	2	5 to 7	Anteriorly 8, posteriorly 5.	200 to 250	As far as, or slightly be- yond, excretory canals	3 to 10	Dog, cat	N. America.
<i>compactum</i> Millzner, 1926	5 to 15	2	6	Anteriorly 15, posteriorly 9.	140 to 200	Not reaching excretory canals	2 to 10	Cat	N. America.
<i>diffusum</i> Millzner, 1926	7 to 15	2.5	6 [- 8]	Anteriorly 9, posteriorly 5.	160 to 250	Reaching, but usually not crossing, excretory canals	3 to 10	Cat	N. America.
<i>longulum</i> Millzner, 1926	5 to 12	2.3	5	Anteriorly 7, posteriorly 5.	180 to 240	Nearly or quite reaching excretory canals	1 to 12	Cat	N. America.
<i>crassum</i> Millzner, 1926	10 to 30	2	5 [- 7]	Anteriorly 10, posteriorly 4.	150 to 175	Reaching excretory canals	6 to 15	Dog	N. America.
<i>halli</i> Tubangui, 1925	—	1	8	—	100 to 140	Considerably beyond excretory canals	5 to 7	Cat	Philippines.
<i>buencaninovi</i> Tubangui, 1925	3	0.9	4 to 5	Anteriorly 7, posteriorly smaller.	150 to 180	Not beyond excretory canals	3 to 12	Dog	Philippines.
<i>Joyceia</i> : <i>chyeri</i> (v. Rátz, 1897)	12 to 20	1.4 to 1.6	13 to 14	Anteriorly 14, posteriorly 10.5 or less.	45 to 50	Beyond excretory canals	1	Cat	Hungary (?)
<i>pasqualei</i> (1893)	20 to 30	1 to 2	16	7	50 (?)	Nearly or quite reach- ing, but not passing, excretory canals	1	Cat	Egypt.
<i>Diplopidium</i> : <i>trinchesei</i> (1892)	1.2 to 7.5	0.7	4	36	25 to 32	Nearly reaching middle line of segment	1	Cat	S. Europe, Egypt.
<i>quinquecoronatum</i> (Rodriguez and Muñoz, 1922)	3.2 to 6.5	0.75	5	Anteriorly 08 to 71, posteriorly 12.8 to 16.	46 to 58	Like that of <i>D. trinchesei</i>	1	Cat	Spain.
<i>milleri</i> (Skrjabin, 1924)	4 to 5.5	0.85 to 1.1	3 to 4	Anteriorly 48 to 53, posteriorly 10.	12 to 16 in young, more in older segments	Nearly reaching middle line of segment	1	Cat	Turkestan.

The adults of these two genera occur in mammals and birds. Their cysticercoids, in some cases, have been found in small cold-blooded vertebrates. The larval forms of both *Joyeuxia chyzeri* and *Diplopylidium trinchessii* apparently occur in various lizards, snakes and batrachians, one of the intermediate hosts being the common gecko, *Tarentola mauritanica*, which, in countries bordering on the Mediterranean, is considerably preyed upon by cats.

The genus **Metroliaesthes** Ransom, 1900, is placed in the subfamily Paruteriniæ, on account of the presence, in gravid segments, of a paruterine organ in front of the uterus, eventually becoming transformed into a spherical or oval egg-capsule. In this genus the scolex is unarmed and without a rostellum. The genital pores are single and irregularly alternating. Each mature segment contains some twenty to forty testes. The uterus is single in origin, but when fully developed consists of two spherical sacs partly fused in the middle line.

Metroliaesthes lucida Ransom, 1900, occurs in the turkey and fowl in North America, India and Africa. The strobila is about 20 mm. long and 1.5 to 1.8 mm. in maximum width. Anteriorly the segments are wider than long, but posteriorly they become nearly twice as long as broad. The scolex measures 0.75 mm. in diameter, and the suckers 0.2 to 0.25 mm. The genital pores are often prominent. The cirrus-sac measures about 0.4×0.1 mm. The testes in each mature segment number up to about thirty-five or forty. The ovary is situated in the middle line of the segment.

HYMENOLEPIDIDÆ.

In the family **Hymenolepididæ** the scolex may be provided with an armed rostellum, or the rostellum may be absent or rudimentary and unarmed. In certain cases the scolex is lost at an early stage in the development of the adult worm, and the succeeding portion of the strobila (the "neck") becomes modified into a "holdfast" or pseudoscolex. The suckers are usually unarmed. The number of testes in each mature segment is small (usually from one to three). The uterus is generally persistent and sac-like. The eggs are usually enclosed in thin, membranous envelopes.

In **Hymenolepis** Weinland, 1858, the rostellum is armed with a single crown of hooks (which are frequently "spanner-shaped," having a short blade and ventral root and a long dorsal root), or is rudimentary and unarmed. The suckers are occasionally spiny. There are three testes in

each mature segment. Their arrangement is variable.* The vas deferens forms both an internal and an external vesicula seminalis. The adults occur in birds and mammals. The development usually involves an intermediate host—generally an Arthropod (insect, crustacean, or myriopod). In certain species, however, no alternation of hosts appears to be necessary, the cysticeroid developing in the villi of the intestinal mucous membrane of the definitive host. It is almost certain, however, that this cannot take place without the eggs first reaching the exterior and being taken in by the mouth.

Hymenolepis nana (v. Siebold, 1852) is of wide distribution, especially in warm climates, throughout the world, occurring in the small intestine

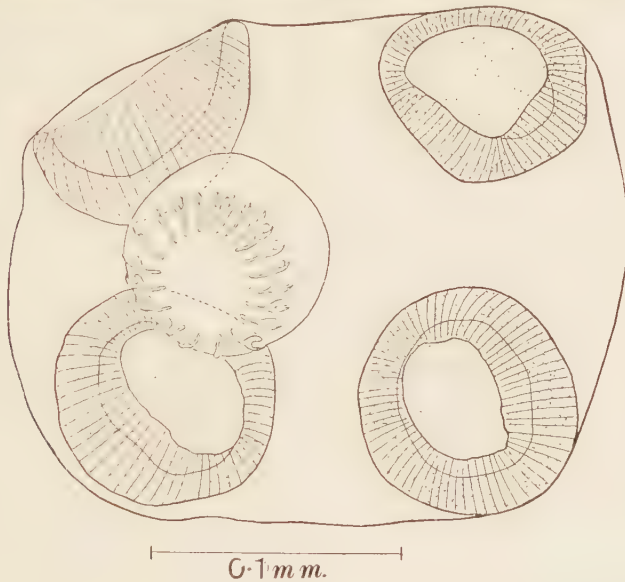


FIG. 76.—*Hymenolepis nana*: SCOLEX, WITH EVAGINATED ROSTELLUM, VIEWED *en face*. (AFTER BAYLIS.)

of man, and being especially common in children. It is a rather small, slender worm, its length, according to state of contraction and number of

* In a recent revision of the species of *Hymenolepis* occurring in birds, Mayhew (1925) has proposed the restriction of the genus to forms in which the three testes are arranged in a transverse row. He has proposed a new genus, *Weinlandia*, for forms in which two of the testes are near the posterior border of the segment, while the third lies more or less in front of the aporal posterior testis. Forms in which the position of the three testes varies in different segments of the strobila are referred by Mayhew to a third genus, *Wardium*. It appears doubtful whether, in different states of contraction, the testes even of a single individual maintain a sufficiently constant position for such a classification to have any definite value. In any case, groups based primarily upon this character should probably not be given higher rank than that of subgenera of *Hymenolepis*.

segments, varying between approximately 7 and 80 mm. or even 140 mm. The maximum width of the strobila is 0.27 to 0.65 mm. The size of the scolex is very variable (diameter 0.13 to 0.4 mm.), as are also the diameter of the rostellum (0.05 to 0.08 mm.), and that of the suckers (0.05 to 0.093 mm.). The rostellum is armed with twenty to twenty-six hooks (usually twenty-two), having a length of 0.016 to 0.020 mm. The number of segments in the strobila varies from less than 100 to more than 800. The eggs have a thin outer envelope measuring 0.048 to 0.06×0.036 to 0.048 mm., and a thicker, somewhat lemon-shaped, inner shell measuring 0.027 to 0.036×0.0225 to 0.0285 mm. The inner shell is provided at the poles with slight knob-like thickenings from which several filaments may generally be seen to proceed. The embryos measure 0.024 to 0.035 mm. $\times$ 0.021 to 0.027 mm., and the embryonic hooks are 0.0105 to 0.015 mm. in length.

It is still a debated question whether a form (previously known as *Tænia murina* Dujardin, 1845, or *Hymenolepis nana*, var. *fraterna*

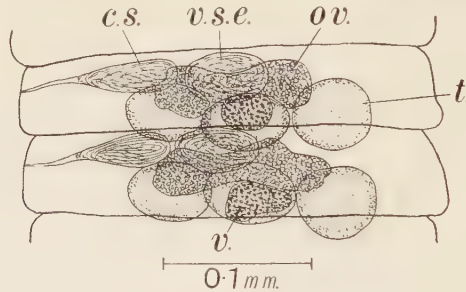


FIG. 77.—*Hymenolepis nana*: TWO MATURE SEGMENTS, DORSAL VIEW
(AFTER BAYLIS.)

c.s., cirrus-sac; ov., ovary; t., testis; v., vitellarium; v.s.e., external seminal vesicle.

Stiles, 1906) which occurs in rats and mice, and which is generally admitted to be morphologically indistinguishable from the human form of *H. nana*, is specifically distinct or not. The recognition of "physiological host-races" of helminths as distinct species is a questionable procedure, even were the evidence of the existence of such races more conclusive than it is at present in the case of *H. nana*. Whatever may be the ultimate solution of this question, it appears highly probable that rats and mice act as disseminators of the human parasite. Joyeux has endeavoured to uphold, on experimental and other grounds, the view that the human form of *H. nana* is a distinct species which had its origin in the rodent form and has developed physiological differences in adaptation to a different host. Joyeux was unsuccessful in his attempts to infect rodents experimentally with the human form. Other observers, however, appear

to have succeeded in similar experiments, and the recent work of Woodland, which was apparently carefully controlled, seems to show that the human form is capable, at least occasionally, of reaching maturity in mice. Still more recently (1927) Chandler has brought forward interesting epidemiological evidence in support of the view that in India the regional prevalence of human infection with *H. nana* is correlated with the prevalence of rats and mice, and that these animals are important factors in its dissemination.

Hymenolepis nana (or at least the form of it which occurs in rodents) is of considerable interest as one of the few Cestodes known to be capable of completing their life-history without a change of hosts.* The embryos, if ingested by the same host in which the parent form developed, settle in the villi of the intestinal mucous membrane, and there develop into cysticercoids. These subsequently escape into the lumen of the intestine and become adult worms. It is almost certain, though not definitely established, that the same life-history applies to the worm in man, and the possibility of frequent auto-infection would explain the very heavy infections sometimes met with in children.

Hymenolepis diminuta (Rudolphi, 1819)
(synonyms: *Tænia flavopunctata* Weinland, 1858;

T. varesina Parona, 1884) is a species whose normal definitive hosts are unquestionably rats and mice. It has, however, been found on several occasions in man (usually in children) in Southern Europe, North and South America, the West Indies, Africa and Japan. Its habitat is the small intestine. It is a much larger worm than *H. nana*, measuring 20 to 60 cm. in length, and having a maximum width of about 3.5 mm. The strobila contains from 600 to 1,000 segments, all of which are considerably wider than long. The scolex has a diameter of 0.2 to 0.5 mm., and bears an unarmed, rudimentary rostellum. The eggs are rounded or oval, with a thickened, yellowish outer membrane, having a maximum diameter of about 0.05 to 0.086 mm., and showing faint radial striations. The inner shell is oval, measuring about 0.028 to 0.035 × 0.022 to 0.028 mm., and has knob-like thickenings at the poles. The embryos measure 0.024 to 0.036 × 0.021 to 0.028 mm., and their hooks are about 0.011 mm. in length.

The cysticercoid of this species has been found in the body-cavity

* Baicalupo, however, has recently claimed to have infected mealworm beetles (*Tenebrio molitor* and *T. obscurus*) with the cysticercoids of the human form of *H. nana*.



FIG. 78.—*Hymenolepis nana*: EGG. (FROM BRUMPT. AFTER JOYEUX.)

of various insects—the meal-moth (*Asopia farinalis*), an earwig (*Anisoblabis annulipes*), certain beetles (*Akis spinosa*, *Scaurus striatus* and the mealworm beetle, *Tenebrio molitor*), rat-fleas (*Ceratophyllus fasciatus*, *Xenopsylla cheopis*)—and also in a myriopod.* Infection, normally in rodents, and accidentally in man, doubtless takes place through the ingestion of these intermediate hosts.

A large number of species of *Hymenolepis* occurs in poultry. Some of the distinguishing characters of the forms occurring in the fowl and those in domesticated members of the duck tribe are given in the two following tables:

TABLE IV.—SPECIES OF *HYMENOLEPIS* IN THE FOWL.

Species.	Length in Mm.	Maximum Width in Mm.	Number of Hooks.	Length of Hooks in μ .	Extent of Cirrus-Sac.	Distribution.
<i>Hymenolepis</i> : <i>cantianiana</i> (Polonio, 1860)	2 to 12	0.4	None	—	Half-way across seg- ment	Europe, Brazil.
<i>exilis</i> (Dujardin, 1845)	20	0.95	60	8	—	Europe.
<i>villosa</i> (Bloch, 1782)†	Up to 200	0.8 to 2	14	20	To aporal excretory canals	Europe, Asia, N. Africa.
<i>tichodroma</i> Fuhrmann, 1901	6 to 8	0.68	11	—	—	Germany.
<i>inermis</i> Yoshida, 1910	5 to 10	0.35	None	—	Nearly half- way across segment	Japan.
<i>exigua</i> Yoshida, 1910	2 to 7	0.3 to 0.4	10	30 to 50	To aporal excretory canals	Japan.
<i>pullæ</i> Cholodkowsky, 1912	100	0.4	—	—	—	Russia.
<i>bauchei</i> Joyeux, 1924	5 to 6	1	35	67 to 70	Across two- thirds of segment	Indo-China.
<i>fedtschenkowi</i> Soloviev, 1911	200	1.5	10	11	—	Russian Turkestan.
<i>carioca</i> (Magalhães, 1898)	30 to 80	0.5 to 0.7	None	—	Half-way across seg- ment	Cosmo- politan.
<i>rustica</i> Meggitt, 1926	4 to 25	6	None	—	To aporal excretory canals	Burma.

Two species of *Hymenolepis* have been recorded from the turkey in the Ural by Clerc. These are **H. meleagris** (Clerc, 1902) and **H. musculosa** (Clerc, 1903). The former is very imperfectly described, but is said

* The following additional intermediate hosts have been reported in Japan by Hongo: *Aglossa dimidiata*, *Tribolium ferrugineum*, *Paralipsa gularis*, *Tinea granella* and several undetermined insect larvæ.

† This species is remarkable in having the aporal border of each segment produced into a long process.

TABLE V.—SPECIES OF *HYMENOLEPIS* IN THE DUCK, GOOSE AND SWAN.

Species.	Length in Mm.	Maximum Width in Mm.	Number of Hooks.	Length of Hooks in μ .	Extent of Cirrus-Sac.	Known or Probable Inter- mediate Host.	Domestic Hosts.
<i>Hymenolepis</i> :							
<i>lanceolata</i> (Bloch, 1782)	30 to 130	5 to 18	8	31 to 35	0.8 to 1.2 mm. long	<i>Diaptomus spinosus</i> , vari- ous Cyclopidae	Duck, goose.
<i>aquabilis</i> (Rudolphi, 1810)	150	3.2 to 4.6	10	27 to 32	A little beyond lateral excretory canals	Swan.	
<i>anatina</i> (Krabbe, 1869)	200 to 300	2 to 3	10	65 to 72	A little beyond lateral excretory canals	<i>Cyprina ophthalmica</i> , <i>Cypris</i> Duck, goose, swan.	
<i>setigera</i> (Frölich, 1789)	200	1 to 3	10	35 to 44	About one-third width of segment	<i>Cyclops brevicaudatus</i> , Goose, swan. <i>Diaptomus</i> spp.	
<i>tenuirostris</i> (Rudolphi, 1819)	100 to 125	1 to 3	10	20 to 23	—	<i>Gammarus pulex</i> , <i>Cyclops</i> Goose. spp.	
<i>fasciata</i> (Rudolphi, 1810)	50 to 160	1 to 2	8	57 to 60	Almost reaches opposite margin	<i>Cyclops agilis</i> , <i>Diaptomus</i> Goose. sp.	
<i>coronula</i> (Dujardin, 1845)	120 to 190	3	20 [? 18 to 26]	12.8 to 17.6	0.3 mm. long	<i>Cyprina ophthalmica</i> , <i>Cypris</i> Duck. <i>ovum</i> , <i>Candona candida</i> , <i>Cyclocypris</i> spp.	
<i>gracilis</i> (Zeder, 1803)	120 to 270	1.5 to 2	8	76 to 82	0.5 mm. long	<i>Candona rostrata</i> , <i>Cyprina</i> Duck, goose. <i>ophthalmica</i> , <i>Cyclops viri-</i> <i>dis</i> , <i>Diaptomus</i> spp.	
<i>megalops</i> (Nitzsch, 1829)	35 to 54	0.75	None	—	Obliquely to near an- terior border of seg- ment	Duck.	
<i>pareula</i> Kowalevski, 1904	1.7	0.25	10	38 to 39	Almost reaches opposite margin (slightly sig- moid)	<i>Herpobdella octoculata</i> Duck.	
<i>collaris</i> (Batsch, 1786)	50 to 160	1 to 2	10	51 to 61	Extends beyond middle line of segment	<i>Gammarus pulex</i> , <i>Cyclops</i> Duck, goose spp., <i>Diaptomus</i> spp.	

Weinlandia

to be very similar to *H. gracilis* (see Table V). *H. musculosa* is a form measuring up to 50 mm. in length and 2 to 3.8 mm. in maximum width, and having very highly developed longitudinal-muscles. The rostellum is armed with ten hooks, 0.0304 mm. in length.

The intermediate host of *Hymenolepis carioca* of the fowl is said to be the stable-fly (*Stomoxys calcitrans*). The intermediate hosts of the forms occurring in ducks and related birds are always, so far as is known, small fresh-water crustacea, mainly "water-fleas" or Copepods. One of

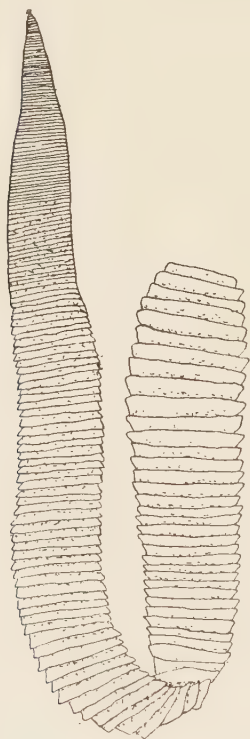


FIG. 79.—*Hymenolepis lanceolata*: ENTIRE WORM. (FROM STILES, AFTER GOEZE.)



FIG. 80.—*Hymenolepis lanceolata*: HOOKS FROM ROSTELLUM. (AFTER KRABBE.)



FIG. 81.—*Hymenolepis gracilis*: HOOK FROM ROSTELLUM. (AFTER KRABBE.)

these species (*H. lanceolata*) is said to have occurred in man, though normally a parasite of ducks and geese. Its supposed occurrence in man is based on a record of the evacuation of two specimens at different times by a twelve-year-old boy at Breslau. Human infection with this worm, if it does occur, must be the result of drinking water containing "water-fleas." This species is sometimes placed in a special genus or subgenus (*Drepanidotænia* Railliet, 1892), on account of the fact that the ovary is placed on the side of the testes remote from the genital pore, and not,

as in most species of *Hymenolepis*, between the testes, and perhaps also on account of the unusually broad, lancet-like shape of the strobila.

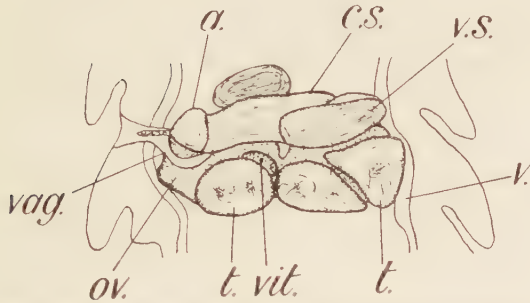


FIG. 82.—*Hymenolepis gracilis*: MATURE SEGMENT (AFTER MEGGITT.)

a., accessory sac; c.s., cirrus-sac; ov., ovary; t., t., testes; v., ventral canal; vit., vitellarium; v.s., external seminal vesicle.

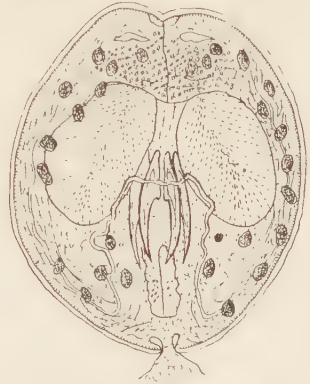


FIG. 83.—*Hymenolepis gracilis*. CYSTICERCOID. (FROM STILES, AFTER MRAZEK.)

The genus **Echinocotyle** Blanchard, 1891, closely resembles *Hymenolepis* in most respects, but has large, oval suckers armed round their edges and in the centre with several rows of minute hooks. The rostellum has ten hooks. There are three testes in each mature segment, as in *Hymenolepis*. In connection with the genital atrium, as in some species of *Hymenolepis*, there is a muscular accessory sac lined with spines.

E. rosseteri Blanchard, 1891, is an apparently rare parasite of the duck, originally recorded from Canterbury, England, but possibly introduced from India. In this species the rostellar hooks measure 0.031 to 0.038 mm. in length. The cysticercoid occurs in Copepods (*Cyclocypris globosa*, *Cypria ophthalmica*).

Fimbriaria Frölich, 1802, is a genus remarkable for the fact that the "neck," consisting of the segments immediately succeeding the scolex in the adult form, is modified into a peculiar, folded expansion, serving as a "holdfast" or "pseudoscolex," the actual scolex being, in fact, generally lost. The rostellum, when present, is armed with a single row of hooks. The

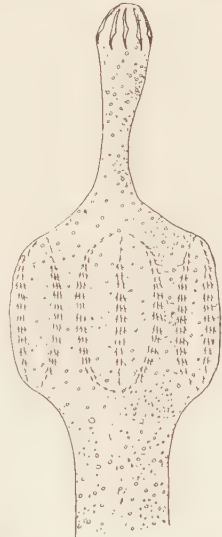


FIG. 84. —*Echinocotyle rosseteri*: SCOLEX. (AFTER BLANCHARD.)

segmentation of the strobila is imperfect, and is largely obscured by secondary transverse divisions and folds. The genital pores are unilateral, and there are three testes for every cirrus-sac. The ovary and uterus are of reticulate form. The former may be, and the latter is

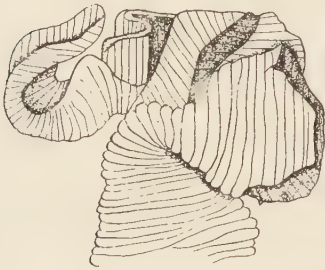


FIG. 85.—*Fimbriaria fasciolaris*:
PSEUDOSCOLEX. (FROM MEG-
GITT, AFTER WOLFFHÜGEL.)

invariably, continuous throughout the strobila. The uterus, however, subsequently breaks up into separate tubular portions, each containing several eggs. Other peculiarities of the genus are that the strobila contains only a single layer of longitudinal muscles, and that there are from six to eleven pairs of longitudinal excretory canals. The adult worms occur in birds.

***Fimbriaria fasciolaris* (Pallas, 1781)**

is a parasite of the duck, goose, fowl, and many species of wild birds, chiefly belonging to the duck tribe. It is a form of very variable size and appearance, measuring 25 to 425 mm. in length and 0.7 to 5 mm. in maximum width. There are ten rostellar hooks, measuring 0.017 to 0.022 mm. in length. The eggs measure 0.035 to 0.045 mm. in diameter. The cysticercoid occurs in a "water-flea," *Diaptomus vulgaris*.

TÆNIIDÆ.

In the family **Tæniidæ** the rostellum is usually well developed and armed with two alternating crowns of hooks of two sizes. Exceptionally there is only a single crown of hooks, or the rostellum is unarmed and rudimentary. The suckers are unarmed. The strobila is usually long and composed of very numerous segments. There is a single set of genital organs in each segment, and the genital pores are irregularly alternating. The testes are numerous. The ovary is bilobed and is usually situated behind the testes, near the posterior end of the segment. The gravid segments are longer than broad, and the uterus consists of a median longitudinal stem which at first is simple, but later sends out a number of lateral branches which may again be branched. The eggs are generally provided with a thick, radially striated inner shell (embryophore). The adult worms occur in mammals and birds.

The larval forms are of various types, ranging from a typical cysticercus, in which a single scolex is developed, to a large bladder (hydatid) in the interior of which are formed large numbers of scolices. They occur chiefly in the connective tissue of mammals.

The genus **Tænia** Linnæus, 1758, is typical of the family. In the sense in which it will be understood here, it includes both forms having a rostellum with a double crown of hooks, and forms in which, in the adult state, the rostellum is rudimentary and hooks are absent. The strobila usually contains a very large number of segments. The adult stage occurs only in mammals, chiefly primates and carnivores.

Attempts have been made to split up the genus into several more restricted genera, based either on the presence or absence of hooks in the adult, or on the characters of the larval forms. Thus the forms typified by *T. saginata* are regarded by some authorities as a distinct genus (*Taniarhynchus* Weinland, 1858), on the ground that hooks are absent in the adult. Since, however, it was shown by Leuckart that the rudiments of hooks were present in the *Cysticercus*, and since the anatomy of the segments in the adult strobila shows no important departures whatever from that of typical species of *Tænia* like *T. solium*, such a distinction is, in the writer's view at least, unjustifiable. Nor does it appear a practical system to base generic distinctions on larval characters, where the adult forms, in the absence of knowledge of the larvæ from which they are derived, cannot with any certainty be generically separated. Names such as *Cænurus* Rudolphi, *Multiceps* Goeze, *Polycephalus* Zeder, *Hydatigera* Lamarck or *Reditania* Sambon, so far as they are applied to adult forms, are therefore here treated as synonyms of *Tænia*.

The larval forms of *Tænia* show a variety of modifications. Typically the larva is a cysticercus with a single invaginated scolex, not undergoing further development until ingested by the final host (*Tænia* in the restricted sense). The scolex of the cysticercus may in some cases become evaginated and a chain of segments (without sexual organs) may be developed while still in the body of the intermediate host. This is the case, for example, with *Tænia taniaformis* of the cat. This type of larva has been termed by Sambon a *strobilocercus*, and its adult form has by some been considered worthy of generic or subgeneric rank on account of the peculiarities of the larva (*Hydatigera*, *Reditania*). In a third type of larva the "bladder" produces internally several or numerous scolices, and to forms of this type the name *Cænurus* has been given, while the corresponding adult forms have been called *Polycephalus* or *Multiceps*.

The adult form of **Tænia solium** Linnæus, 1758, the type species of the genus, is known only in man, its habitat being the upper part of the small intestine. The usual length of the strobila is from 2 to 3·5 metres, though in exceptional cases it may grow to a length even of 8 metres. The maximum width is about 8 mm., and the number of segments rarely exceeds 900. The scolex is globular and about 0·6 to 1 mm. in diameter. It sometimes exhibits some dark pigmentation. The rostellum bears

two crowns of hooks, of which there are twenty-two to thirty-two (usually twenty-six or twenty-eight). These hooks are of two kinds, arranged alternately, measuring 0.16 to 0.18 and 0.11 to 0.14 mm. in length respectively. The suckers have a diameter of 0.4 to 0.5 mm. The



FIG. 86.—*Tania solium*: THE TWO CROWNS OF ROSTELLAR HOOKS, VIEWED *en face*. (AFTER STEIN.)

mature segments are of approximately equal length and breadth. The gravid segments are considerably longer than broad (about 10×5 mm.). The uterus generally has from seven to twelve main branches on each side. The eggs have a thin outer envelope and a thick, subglobular, radially striated inner shell or embryophore. The latter has a diameter of 0.031 to 0.036 mm., while that of the embryo is about 0.02 mm.

The cysticercus, commonly known as *Cysticercus cellulosæ*, is an elliptical bladder-like organism measuring 6 to 20×5 to 10 mm. and containing a single invaginated scolex. It occurs chiefly in the intermuscular connective tissue of the pig, in which it is the cause of the appearance known as "measles" ("measly pork"). Human infection is usually acquired

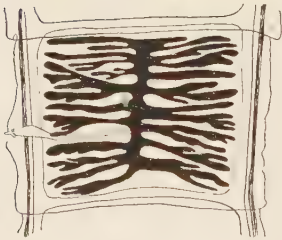


FIG. 87.—*Tania solium*: GRAVID SEGMENT. (AFTER STILES, MODIFIED.)

The uterus is represented in solid black.



FIG. 88.—*Tania saginata*: GRAVID SEGMENT, FOR COMPARISON WITH FIG. 87. (AFTER STILES, MODIFIED.)

by the consumption of pork in an insufficiently cooked condition, and the species, though of world-wide distribution, is relatively rare except in localities where many pigs are kept and where pork is eaten raw or nearly so. It appears to be much less common in Europe than formerly. In Portugal, however, it is said to be still more common than

T. saginata, which is the species usually encountered elsewhere. In addition to the domestic pig, a variety of other animals have been recorded as intermediate hosts for this worm, but the specific determination of the cysticercus must in many cases be regarded with suspicion. These animals include the wild boar, ox, buffalo, Bactrian camel, roe-deer, goat, sheep, horse, dog, cat, polecat, brown bear, hare, rat and various monkeys. The cysticercus also, not infrequently, occurs in man, and there is a danger of auto-infection with the larval form in the case of persons harbouring the adult.

Tænia saginata Goeze, 1782, which also occurs in the intestine of man, is a much commoner species in most localities than *T. solium*, and is of world-wide distribution, occurring wherever beef is eaten. It is a larger form, on the average, than *T. solium*, from which it differs also notably

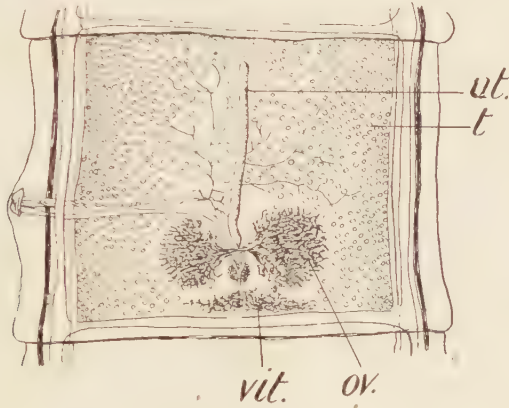


FIG. 89.—*Tænia saginata*: MATURE SEGMENT. (AFTER STILES.)

ov., ovary; t., testes; ut., uterus; vit., vitellarium.

in having no rostellum or hooks in the adult condition. The scolex is relatively large, measuring 1.5 to 2 mm. in diameter, and is somewhat flattened anteriorly. It occasionally shows some pigmentation, which may even extend also to some of the mature segments. The length of the strobila is very variable, usually between 3 and 8 metres, but sometimes attaining as much as 10 metres. The maximum width is 12 to 14 mm., and the number of segments may be as large as 1,200 or 1,300. The uterus has generally from fifteen to thirty-five main lateral branches on each side. The gravid segments are frequently liberated singly, and have considerable power of independent movement after being evacuated. They may measure as much as 18 to 20 × 5 to 7 mm. The embryophores are oval, measuring 0.03 to 0.05 × 0.02 to 0.03 mm.

The cysticercus (known as *Cysticercus bovis*) is very similar to that of

T. solium, and occurs chiefly in the ox, usually in the intermuscular connective tissue, especially of the muscles of the jaw, tongue, heart and diaphragm, but also sometimes in other organs, such as the lungs and liver. It measures about 7.5 to 9×5.5 mm. In addition to cattle, the larva has been recorded from various other ruminants (sheep, goat, llama, giraffe, North American prong-horn antelope), but some of the determinations are open to question. The same probably applies to the few cases in which this cysticercus has been described as occurring in the brain or eye of man. In any case, if it actually occurs in man, it does so much more rarely than *C. cellulosæ*.

The adult form of *T. saginata* is subject to much variation in size and general appearance, in the shape and size of the segments, and in the mode of branching of the uterus and other details of anatomy, while

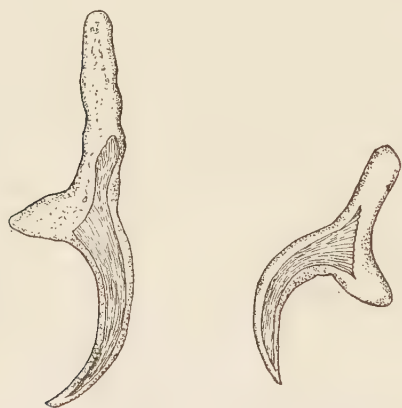


FIG. 90.—*Tania hydatigena*: LARGE AND SMALL HOOKS FROM ROSTELLUM. (AFTER HALL.)

many kinds of malformation in the strobila and in individual segments have been recorded. It is probable that these facts, together with the immense differences in appearance possible in different states of preservation and degrees of contraction, have led to the description of a number of spurious species. At all events, several forms from man have been described whose specific distinctness from *T. saginata* appears to rest upon somewhat doubtful evidence. Such forms are *T. africana* v. Linstow, 1900; *T. hominis* v. Linstow, 1902; *T. confusa* Ward, 1896;

T. tonkinensis Railliet and Henry, 1905; *T. philippina* Garrison, 1907; *T. bremneri* Stephens, 1908. Several of these have been recorded only once or twice, while some are based on fragmentary material.

The name *Tania infantis* has been given by Bacigalupo (1922) to a tapeworm found in a five-year-old child at Buenos Aires. Bacigalupo's description has not been seen in the original by the writer, but from an abstract of it in the *Journal of Parasitology* it appears doubtful whether the species is distinct from *T. tæniæformis* of the cat. The only character mentioned in the abstract which is not quite normal for *T. tæniæformis* is the large size of the scolex (diameter 3 mm.).

A number of species of *Tania* occur as adults in the dog and cat. It is impossible to give specific descriptions of all of them, but some of their characters are given in Table VI (p. 115). It is by no means easy to

TABLE VI.—SPECIES OF *TENIA* (SENS. LAT.) PARASITIC, AS ADULTS, IN THE DOG AND CAT.

Species.	Length of Strobila in Cm.	Maximum Width of Strobila in Mm.	Number of Hooks on Rostellum.	Length of Large Hooks in μ .	Length of Small Hooks in μ .	Approximate Number of Testes in each Mature Segment.	Number of Main Branches on each Side of Uterus.	Domesticated Hosts of Adult Form.	Known Distribution.
<i>Tænia</i> :									
<i>balaniceps</i> Hall, 1910	24 or more	4	28 to 32	145	93 to 98	Numerous	Numerous	Dog	North America.
<i>brachysoma</i> Setti, 1899	10	3	30 to 32	135 to 145	95 to 105	—	About 18	Dog	Italy.
<i>brauni</i> Setti, 1897	15 to 18	6	30	95 to 140	70 to 90	—	—	Dog	Africa (Eritrea).
<i>hydatigena</i> Pallas, 1766	75 to 500	7.5	26 to 44	170 to 220	110 to 160	600 to 700	5 to 10	Dog, ? cat	Cosmopolitan.
<i>krabbei</i> Moniez, 1879	20 or more	About 9	26 to 34	148 to 170	85 to 120	260	9 to 10	Dog	Iceland, Alaska.
<i>ovis</i> (Cobbold, 1869)	45 to 110	4 to 8.5	24 to 36	156 to 188	96 to 128	300	20 to 25	Dog	Europe, Africa, N. America, New Zealand.
<i>pisiformis</i> (Bloch, 1780)	60 to 200	4.8	34 to 48	225 to 294	132 to 177	400 to 500	8 to 14	Dog, rarely cat	Cosmopolitan.
(= <i>serrata</i> Rud.)									
<i>antarctica</i> Fuhrmann, 1920	25	6 to 7	28 to 34	144 to 156	92 to 102	500	13 to 15	Dog	Antarctic region.
<i>novella</i> Neumann, 1896*	0.6 to 3.3	1.13	40 to 42	250 to 260	150 to 155	—	—	Cat	Europe.
<i>teniae ornis</i> (Batsch, 1786)	15 to 60	5 to 6	26 to 52	380 to 420	250 to 270	Numerous	Numerous	Cat	Cosmopolitan.
(= <i>crassicolis</i> Rud.)									
<i>multiceps</i> Leske, 1780	40 to 100	5	22 to 32	150 to 170	90 to 130	200	9 to 26	Dog	Cosmopolitan.
(= <i>caninus, cerebralis</i>)									
<i>serialis</i> (Gervais, 1847)	20 to 72	3.5 to 5	26 to 32	135 to 175	78 to 120	Numerous	20 to 25, anastomosing	Dog	Cosmopolitan.
<i>gaigieri</i> (Hall, 1916)	25 to 182	5	28 to 32	160 to 180	115 to 150	200 to 225	12 to 15	Dog	India, Ceylon.

* Immature, probably an accidental parasite. Neumann considers it closely related to *T. pisiformis*.*Multiceps*

distinguish several of these species in the adult stage, there being considerable variation in almost all the characters upon which specific determination must rely, such as the number and size of the rostellar hooks, number of uterine branches, etc. A full and valuable account of these forms has been given by Hall.* As in the case of *Dipylidium*, it seems possible that some of the supposed species may be found to be untenable.

Some brief notes on the larval forms and intermediate hosts of these species from domestic carnivores, so far as they are known, may be given :

- T. hydatigena*. Cysticercus (" *C. tenuicollis* ") with relatively large bladder, occurring in the liver, or in the abdominal cavity (free or attached to viscera) of ungulates, also of primates and rodents. Domestic hosts of larval form: Ox, sheep, goat, pig. Recorded also in dog and cat, and doubtfully in man.
- T. krabbei*. Cysticercus (" *C. tarandi* ") in muscles of reindeer.
- T. ovis*. Cysticercus (" *C. ovis* ") in heart and other muscles, lungs, etc., of sheep and goat.
- T. pisiformis*. Cysticercus (" *C. pisiformis* ") in liver, mesentery or abdominal cavity (free or attached to viscera) of rodents, chiefly rabbits and hares. Doubtfully recorded in man.
- T. tæniæformis*. Strobilocercus (" *Cysticercus fasciolaris* ") in liver and abdominal cavity of small mammals (chiefly rats and mice).
- T. multiceps*. Cœnurus (" *C. cerebralis* ") in central nervous system of various ungulates, including sheep, goat, ox and horse. Recorded also in pig, rabbit, hare and man.
- T. gaigeri*. Cœnurus in central nervous system, liver, lungs, etc., or in connective tissue, of goat.
- T. serialis*. Cœnurus in connective tissue (especially subcutaneous tissue) of rodents, chiefly rabbits and hares. Recorded also in horse and doubtfully in goat.
- T. brauni*. von Linstow, in 1902, identified with this species a bladderworm found under the skin of an Egyptian gerbil. This resembled a Cœnurus in having numerous scolices, but these were developed externally instead of internally. Railliet and Henry, on other grounds, have suggested that the adult form of *T. brauni* should be regarded as a *Multiceps*, but Hall does not concur in this view.

A Cœnurus originally found in a gerbil, and described under the name of *Multiceps glomeratus* by Railliet and Henry in 1915, has been recorded

* "The adult Tænioid Cestodes of Dogs and Cats, and of related Carnivores in North America." *Proc. U.S. National Museum*, Washington, lv., pp. 1-94 (1919).

once from man by Turner and Leiper (1919). It was found in a tumour in an intercostal muscle of a native of Northern Nigeria. The adult form is unknown.

The genus **Echinococcus** Rudolphi, 1801, differs from *Tania* in the extremely small size of its species in the adult condition, and in the fact that the strobila consists of a very small number of segments (not more than four or five, of which, as a rule, only the posterior segment is gravid). The rostellum bears two crowns of hooks of different sizes. The genital pores are irregularly alternating. More striking characters are found in the larval stage. The larval form is the so-called "hydatid," which is a large bladderworm or "cyst" with a thick, laminated wall, which may give rise, internally or externally, to daughter-cysts. Within the cyst or cysts "brood-capsules" are developed, and each of these contains numerous scolices.

The adult worms occur in the intestine of carnivorous mammals; the larval stages in the tissues of various mammals, chiefly herbivores.

Echinococcus granulosus (Batsch, 1786) is the only form known to occur in man and domestic animals. The adult occurs in the small intestine of the dog, cat and various wild carnivores. It is a very small worm, usually not exceeding 4 to 5 mm. in length, and with three or four segments. The rostellar hooks of the two crowns measure respectively 0.022 to 0.03 and 0.018 to 0.022 mm. (or, according to Leuckart, 0.040 to 0.045 and 0.03 to 0.038 mm.). The suckers are about 0.013 mm. in diameter. The last (gravid) segment is frequently half the length of the whole worm. The mature segment contains about forty to sixty testes, which are congregated for the most part towards the anterior and posterior ends of the segment. The ovary is horseshoe-shaped, with the concavity posterior. The vitelline gland lies behind it, and consists of dorsal and ventral lobes, each being formed of two lateral portions. The eggs measure 0.032 to 0.036 $\times$ 0.025 to 0.03 mm.

The larval form of *E. granulosus* occurs in almost every kind of situation in the body of its hosts. These include man and (among domesticated animals) the ox, sheep, goat, pig, camel, horse, donkey, dog, cat and rabbit. Infection is acquired by the ingestion of eggs derived from the fæces of an infected dog or other animal, and there is reason for believing

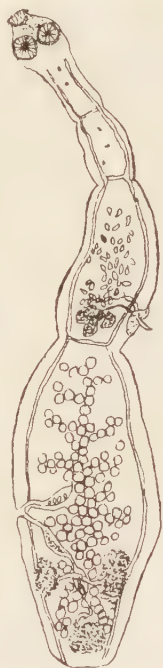


FIG. 91.—*Echinococcus granulosus*: ADULT. (PARTLY AFTER FIEBIGER.)

that where hydatid disease is common in man it is acquired more often through the direct handling of dogs or cats than by contamination of food or water. In Iceland, where *Echinococcus* is very prevalent, Einarsson considers that sheep are even more important than dogs as a factor in the spread of human infection, and that in the case of both animals the chief danger lies in handling the coat. He has shown that in Iceland women are more frequently infected than men, and particularly between the ages of twenty and forty. This is explained by the fact that ewes are kept near the farms, where they are regularly milked by the women and girls, who also do all the shearing. It is chiefly near the farms that the ground is contaminated by dogs, and here the ewes are liable not only to become infested with hydatids but to have their wool soiled with egg-containing material, which is readily transferred to the hands of the women.

The animals most prone to infection with the adult form are naturally sheep-dogs and dogs or cats which have access to slaughterhouse offal.

PART II
ROUNDWORMS

ROUNDWORMS

I. THE THREADWORMS OR NEMATODES (CLASS NEMATODA).

Brief Definition.—Unsegmented “roundworms,” without segmentally arranged appendages, in which the body-wall, covered externally by a homogeneous cuticle and without a cellular epidermis or an epithelial lining, encloses a body-cavity filled with fluid in which the organs float. An alimentary canal is present, but a proboscis absent. Sexes usually separate. Gonads continuous with their ducts. In the male the genital duct opens with the intestine into a common cloaca. In the female the anus and genital aperture are distinct. The group includes both free-living and parasitic members.

The Nematodes are a well-defined group of worms without obvious phylogenetic relationships with any other class of animals. They have been commonly regarded as forming, with certain other groups—the Acanthocephala and the Nematomorpha or Gordiacea—a Phylum to which the name Nemathelminthes has been given; a term indicating worms of thread-like form, and sometimes translated “roundworms.” These terms may be convenient as indicating the shape and appearance of the animals, but neither in their structure nor in their development is there any convincing evidence to be found that the Nematodes are at all closely related to the other groups mentioned. It has been suggested that anatomically they bear more resemblance to the Arthropoda than to any other group, but it must be admitted that this suggestion has only been made *faute de mieux*, and that the relationships of the group, in the absence of palæontological evidence, remain extremely obscure. The Nematoda, in fact, appear to occupy a completely isolated position, and may, for our present purpose, be treated as an independent class of animals.

The group is a remarkably homogeneous one, though extremely rich in genera and species. So large is the number of forms already known that it is considered by some authorities that the Nematodes will ultimately be found to rival, if not exceed, the Insects in numbers. A large proportion of these worms are free-living, and these are found in almost every kind of situation in which animal life is possible. Most of them are adapted for feeding on liquid or semi-solid food by a process of suction, and this is the habit of the majority of the parasitic forms, which have doubtless become gradually adapted to life within the bodies of other animals. Some few still exhibit an alternation of a parasitic

with a free-living generation, while many are only parasitic for a portion of their lives, either as larvæ or as adults. Apart from the disappearance of external sense-organs, such as eye-spots and highly developed sensory bristles, which would clearly be of little use to an internal parasite, the truly parasitic forms show very little difference in structure from their free-living relatives. There is little sign of the "degeneration" so commonly associated with a parasitic existence. On the other hand, the reproductive organs, as is usual in such cases, tend to be much more highly developed, a very large number of offspring being produced, and provision thus made against the failure of many of the young to meet with a suitable host.

A typical Nematode is a cylindrical, more or less elongate animal, tapering somewhat towards each end. The body is covered externally with a very tough, resistant and elastic cuticle, sometimes (though rarely in parasitic forms) provided with bristles, especially at or near the extremities. In the cuticle two or more layers can generally be distinguished, and it is usually marked throughout with a regular series of minute, shallow, transverse grooves, called striations. As a rule, during life, it is firm and taut, though occasionally it shows a certain amount of transverse wrinkling, allowing of additional flexibility. In some forms the cuticle is produced into spines or scale-like structures, which probably assist in the process of burrowing among the host's tissues. At the sides of the body the cuticle may be raised into a pair of longitudinal ridges or flanges, termed lateral alæ. These probably serve as "fins" and assist locomotion. Frequently these alæ are well developed only anteriorly, and become insignificant or disappear posteriorly. When confined to the "neck" region they are often called cervical alæ. In the males of many Nematodes there are special lateral expansions of the cuticle in the caudal region, known as caudal alæ, which subserve copulation. In the Strongyloidea a bell-shaped cuticular expansion, called the *bursa*, surrounds the posterior extremity.

The cuticle is secreted by a syncytial protoplasmic layer which lies immediately below it. Below this layer there is a single layer of muscle-cells whose fibres are arranged longitudinally, in such a way as to produce, by their contraction, dorso-ventral bending of the body. Locomotion is thus effected by a series of up-and-down undulations, the animal "swimming" in this way in the surrounding liquid or semi-liquid medium. When placed on a flat surface, covered by a thin film of moisture, a Nematode invariably lies on its side. The muscle-cells take various forms and show various types of arrangement. These were formerly used by Schneider and others as a basis of classification, but have been found to be unsatisfactory for this purpose, as different types may occur in

closely related forms, or even combined within the same species. In the familiar text-book type, *Ascaris*, each muscle-fibre is spindle-shaped and is produced on its inner surface into a large, rounded mass of protoplasm, containing the nucleus and giving off processes which run obliquely or transversely to be inserted into the body-wall at the mid-dorsal and mid-ventral lines. This is an example of the type of musculature termed by Schneider (1866) "polymyarian," in which the muscle-cells are numerous and irregularly arranged. In the "meromyarian" type of Schneider, the musculature is composed of eight longitudinal rows of flat, rhomboidal cells. In Schneider's third type, "holomyarian," the muscles were supposed to be undivided, or divided only in the longitudinal direction. The forms placed in this group, however, have been shown to be really polymyarian. The meromyarian type is recognizable in most of the Strongyloidea, and occurs also in some Ascaroidea, while the polymyarian type occurs not only in many of the Ascaroidea, but also in the Filarioidea.

The musculature of the body-wall is divided, as a rule, into four sectors by four longitudinal internal thickenings of the subcuticular layer. Two of these thickenings, known as the lateral "fields," run along the sides of the body, and are usually well developed and prominent. The others, situated in the mid-dorsal and mid-ventral lines, are less conspicuous. The musculature forms the boundary of a more or less spacious body-cavity, filled with fluid, in which the alimentary canal and the reproductive organs float. The mouth is situated at the anterior end, terminally or subterminally, and may or may not be guarded by lip-like structures. Primitively, there is reason for believing, all Nematodes were provided with three lips, one being dorsal and two subventral. In this and in certain other respects there is evidence of a combination of triradial symmetry with the bilateral symmetry of the body, the latter having possibly, at a remote ancestral period, been superimposed upon the former. In a large number of existing forms, including almost all the free-living and several families of parasitic genera, this three-lipped condition persists with only slight modifications. These forms will be treated here as a single Order, the Ascaroidea. Each of the three lips usually carries on its outer surface two of the six sensory papillæ with which the head is typically provided. In other forms the three lips have given place to a pair of lateral lips, each carrying three of the papillæ referred to. This is the condition characteristic of the family Spiruridæ and several other families. In others, again, the lips have disappeared, the papillæ being found on the general surface of the cuticle in the vicinity of the mouth, while in some cases secondary lip-like structures, independent of the papillæ, have been developed.

The mouth may lead into a special cavity with thickened cuticular or chitinous walls, and with or without various kinds of tooth-like structures or other modifications. When the cuticular wall of this vestibule is independent of a muscular investment, it is conveniently termed a *buccal capsule*. It may, however, be more intimately connected with the œsophagus which follows it, in such a way that it is enclosed in muscles. In this case it will be convenient to refer to it as a *pharynx*. Whether a buccal capsule or pharynx be present or not, there is invariably an *œsophagus* or specialized anterior portion of the alimentary canal. This, or its anterior part, is usually provided with powerful muscular walls, surrounding a three-sided lumen with a cuticular lining. This cuticular lining is a stomodæum—*i.e.*, is continuous with the external integument—and is moulted with the latter at the regular larval ecdyses. The muscles of the œsophagus are so arranged as to dilate the lumen by their contraction, and in this way the organ acts as a suction-pump for taking in liquid food. The walls of the œsophagus commonly contain three glands, one dorsal and two subventral. The dorsal gland opens into the mouth, the others into the lumen of the œsophagus. In some forms there are also cephalic glands (highly developed, for example, in the Ancylostomidæ) lying mainly free in the body-cavity and opening into the mouth. These are believed to secrete a toxic substance.

In many forms there is at the posterior end of the œsophagus a muscular *bulb*, containing a triple arrangement of "valves." In others there may be a specialized posterior portion of the œsophagus, of non-muscular and possibly glandular structure, conveniently termed a *ventriculus*. The œsophagus leads, directly or through the bulb or ventriculus, into the intestine, which is a simple, usually straight tube with a circular or flattened (not three-sided) lumen. Its wall is composed of epithelial cells and is non-muscular. Posteriorly it passes into the proctodæum, which, in the male, is a *cloaca*, or common atrium with which the genital canal is also connected, and, in the female, a short *rectum*, opening at the anus on the ventral surface near the posterior end. In connection with the proctodæum there are frequently three unicellular "rectal glands."

The nervous system consists of a main mass in the form of a ring of fibres surrounding the œsophagus, and connected with groups of ganglionic cells from which as a rule six longitudinal nerve trunks are given off both anteriorly and posteriorly. Of the latter the most important are situated in the mid-dorsal and mid-ventral lines. These are connected at intervals by circular commissures. There is sometimes a ganglion on the ventral nerve near the anus. The only sense-organs universally present are apparently of a tactile nature, and are in the form

of papillæ (or, in many free-living forms, bristles), situated chiefly towards the extremities and each supplied with a special innervation. Those surrounding the mouth (cephalic papillæ) have already been mentioned.* In addition to these there is in almost all parasitic Nematodes a pair of cervical papillæ, situated at the sides of the body in the œsophageal region. In some forms there is also a pair of lateral or subdorsal papillæ in the middle region of the body, called by Seurat the "intestinal papillæ." The caudal end of the male is usually provided with a number of special papillæ, commonly arranged in bilaterally symmetrical pairs, and doubtless concerned in copulation. Some of these are situated in front of the cloacal aperture (preanal) and others on the post-cloacal portion of the body, or tail (postanal). The tail of the female also usually bears a single pair of papilla-like organs, while in some species there may be a pair in the neighbourhood of the vulva. "Eye-spots," or *ocelli*, are present in some free-living Nematodes, and when present, consist of internal masses of pigment, in intimate connection with the œsophagus, and sometimes surmounted by a hyaline mass acting as a lens. Such organs, however, are unknown among truly parasitic forms.

The excretory system, in the more primitive forms, consists of a unicellular gland-like organ, usually situated in the œsophageal region, and connected with the exterior by a minute ventral duct. In the more highly specialized forms, however, including probably all those parasitic in vertebrates, it consists of longitudinal canals contained in the lateral fields, running throughout almost the entire length of the animal and connected in the œsophageal region by a transverse ventral "bridge," where they open into a narrow ventral duct leading to a small excretory pore. In some forms (*Oxyuridæ*) there is a relatively large bladder-like expansion connected with the excretory duct. In certain *Ascaridæ* the excretory system is asymmetrical, the canal of the right side being more or less rudimentary or absent, while that of the left is partly modified into a ribbon-like "gland," and the pore is situated very far forward, sometimes actually between the bases of the ventro-lateral lips. The excretory system contains no cilia or flame-cells. "Phagocytic organs," in the form either of giant cells or of branching plasmodia projecting from the lateral fields into the body-cavity, have been described in certain species. These are supposed to act as filters for removing bacteria or other foreign particles from the body-fluid.

* In free-living forms there is commonly a pair of specialized cephalic "lateral organs" (termed by Cobb "amphids"), and similar organs are said to exist in the larvæ of certain parasitic forms. It appears uncertain whether these organs are homologous with the usual lateral pair of cephalic papillæ,

Special circulatory and respiratory systems are entirely absent. It is possible that the fluid of the body-cavity acts as a vehicle carrying oxygen to the organs bathed in it.

With few exceptions, the sexes are separate among the Nematodes. Hermaphroditism and parthenogenesis occur in certain genera. Among the bisexual forms the males are almost invariably smaller and less numerous than the females. In some cases the difference in size is so marked that the males are liable to be overlooked in collecting, or mistaken for immature forms. The reproductive glands in both sexes are elongate and often much convoluted sac-like organs, closed at the free end and continuous at the other with the ducts by which their products reach the exterior. In the males of some of the free-living forms there are two testes, but in the majority of Nematodes there is but one, connected with a single ejaculatory duct. At the free end of the testis the cells destined to give rise to spermatozoa form a solid column. Towards the other end, spermatocytes in successive stages of development are found, attached, in most families, to a central axis, or *rhachis*. The spermatozoa are, as a rule, unlike those of most other groups of animals in being rounded or amoeboid cells, without tail-like appendages. Specialized regions of the male duct may often be distinguished, and are sometimes referred to as a vas deferens, a seminal vesicle, and an ejaculatory duct, the latter being the muscular posterior portion opening into the cloaca. A pair of "cement glands" is sometimes present, opening into the ejaculatory duct, and producing a substance which serves to attach the male firmly to the female during copulation. In connection with the cloaca there is also usually a sheath, or a pair of such sheaths, containing a copulatory spicule or spicules. These are chitinous structures of very variable form, serving as intromittent organs, though not directly connected with the male duct. Their chief function is probably that of "holdfasts" during copulation, or instruments for expanding the vagina of the female. They may, however, further act as "gutters" along which the sperm is guided, and it has been suggested that they are also used as organs of excitation. Their extrusion and retraction are brought about by special extensor and retractor muscles connected with the sheaths. In many genera there is another chitinous structure (or one or more pairs of such structures) formed as a thickening of the dorsal wall of the cloaca, and often appearing to serve as a guide for the spicules. This is the *accessory piece* or *gubernaculum*. In some forms, especially among the Strongyloidea, a chitinous structure developed in connection with the ventral wall of the cloaca has also been described, and has been named by Hall the *telamon*.

The female genital tubes are, in most cases, paired. The ova are

formed in the ovaries in the same manner as the spermatozoa in the testis of the male, there being, as a rule, a central rhachis. Each ovary is connected by an oviduct with one of the tubular branches of the uterus. There is usually a narrow, muscular vagina, opening at the vulva, which is ventrally situated but very variable in position in different groups. It may be in the middle region of the body (probably its primitive position), or may be far displaced towards either extremity. According to the position of the vulva the uterine branches may run parallel to each other or in opposite directions ("opposed"), and various modifications occur in their arrangement. Generally speaking, the vagina leads into an undivided portion (generally referred to as the "common trunk") of the uterus, and this divides to form two or more branches, each with its separate ovary.

The ova are fertilized in the uterus, and in most cases firm shells of a chitinous substance are afterwards secreted round them. In the more primitive forms (most of the free-living genera and a few parasitic genera among the Rhabditidae and Oxyuridae) the eggs are relatively large and produced in small numbers. In the majority of parasitic forms, however, the females are extremely prolific, many thousands of eggs being produced even in a single day. The development of the embryo within the egg, in some groups, takes place *in utero*. In others it proceeds no further than the earliest segmentation-stages before oviposition.

The larval development of the Nematodes is direct, in the sense that no pronounced metamorphosis is involved, and the larvæ, when hatched, resemble their parents in general form. Four "moult," or ecdyses, usually take place during the growth of the young worms, at which the outer cuticle becomes detached, together with the linings of the mouth, œsophagus and rectum. As each new cuticle is formed, beneath the old one about to be moulted, changes may occur in the structure of the mouth and other parts. The larval life is thus divided by the moults into a series of periods or "stages." The second moult usually marks an important crisis in the existence of a parasitic Nematode, for it is at this stage that it reaches the "infective" period, and, ceasing to live and feed like a free-living form, awaits the opportunity of entering a suitable host. The infective stage is, in some cases, reached before hatching from the egg. Frequently the second cuticle is not shed at once, but is retained as an additional protective envelope or "sheath" until entry into a host is effected. The larva thus protected is sometimes referred to as "encysted," but this is a somewhat misleading term.

The life-history may or may not involve more than one host. When there is but a single host, the second, third and fourth cuticles are usually shed within it, after which the worms attain the adult form, develop to

sexual maturity, pair and reproduce. When there is an intermediate host, this is usually an Arthropod or one of the lower vertebrates, and the second-stage larva generally becomes encapsuled among its organs or in its body-cavity, by the formation round it of an adventitious capsule or "cyst" of tissue derived from the host, and there undergoes the second moult, and, as a third-stage larva, awaits the ingestion of this host by the final host. This is a type of life-history met with chiefly among the Spiruridæ. Among the Filariidæ a somewhat similar life-history prevails, differing, however, in details.

The classification of the Nematodes here followed is that adopted by Baylis and Daubney.* It seems clear that so long as the prevailing practice was followed of treating the parasitic forms separately from the free-living, there could be nothing "natural" in the arrangement. Accordingly, an attempt has been made to treat them together, and the whole group has been divided into five "Orders," partly corresponding with the "Superfamilies" of Railliet and other authors. All these Orders contain parasitic forms of importance for the purpose of this book, and will be defined in the appropriate places in the text.

THE ORDER ASCAROIDEA.

This large group contains all the forms which retain the supposedly primitive characteristic of possessing three lips, of which one is dorsal and two subventral. In some cases the lips may be much reduced or even apparently absent, but more or less clear indications of their original presence can generally be traced.

The order includes the families Ascaridæ, Heterakidæ, Kathlaniidæ, Oxyascaridæ, Oxyuridæ and Atractidæ, the members of which are all parasitic; the families Rhabditidæ, Mermithidæ and Anguillulinidæ, containing a large number of genera which may be either free-living or parasitic (the last-named family chiefly on plants), or may have both free-living and parasitic phases; and several families consisting entirely of free-living forms.

ASCARIDÆ.

The family **Ascaridæ** consists mainly of relatively large, stout forms in which there are three well-defined lips. The dorsal lip bears on its outer surface a pair of papillæ, frequently with double terminations, while each of the subventral lips also has, as a rule, two papillæ, of which that towards the ventral side is large and often double, while that of the other

* *A Synopsis of the Families and Genera of Nematoda.* British Museum (Natural History), 1926.

side is frequently extremely inconspicuous. There may or may not be, on the inner surface of each lip, a transverse series of minute denticles, known as a dentigerous ridge. Between the bases of the main lips three smaller, conical, subsidiary lips, or interlabia, may be present. There is no chitinous buccal capsule or pharynx. The œsophagus is usually simple, club-shaped and muscular, but may be connected posteriorly with a small muscular spherical bulb, without internal valves, or with a specialized granular structure, possibly glandular in function, conveniently termed a ventriculus. In certain forms this ventriculus gives rise to one or more solid appendices of similar histological structure, while there may also be one or more blind anterior prolongations, or cæca, springing from the intestine immediately behind its junction with the œsophagus or ventriculus.

Caudal alæ are usually absent or very slightly developed in the male, but there is usually a large number of caudal papillæ, of which the majority are preanal. The spicules are paired and equal or subequal in length, and may or may not be provided with lateral flanges or alæ. An accessory piece is usually absent. The vulva is usually somewhat in front of the middle of the body. The uterus consists, as a rule, of two parallel branches. Occasionally, however, there are four or six. The worms are oviparous, producing very large numbers of eggs, the contents of which are unsegmented at the time of laying.

In the subfamily **Ascarinæ** the œsophagus is without a well-marked ventriculus, though a small muscular bulb, or even a small granular posterior portion, may be present. An accessory piece is absent. The life-history is direct, no intermediate host being required.

In the genus **Ascaris** Linnaeus, 1758, interlabia are absent or extremely reduced. One or more of the anterior pairs of postanal papillæ in the male have double terminations. The preanal papillæ are numerous and irregularly arranged. The spicules are non-alate, tubular and relatively short and stout. The adult worms occur in the small intestine of mammals.

Ascaris lumbricoides Linnaeus, 1758 (synonyms: *A. suis* Gmelin, 1790; *A. ovis* Rudolphi, 1819; *A. suilla* Dujardin, 1845), the common "roundworm" of man, is of world-wide distribution. It occurs also in the larger apes, in the pig,* occasionally in sheep and cattle, and has

* While there is fairly general agreement that no morphological difference can be detected between the forms found in man and the pig, experimental and epidemiological evidence has led some authorities to regard them as physiologically distinct varieties or races. The question is still an open one, but it is reasonable to suspect that even if certain strains have, in the course of generations, become better adapted to one host than to the other, cross-infections may take place at least occasionally, and the possibility of human infection being acquired through the ingestion of eggs derived from pigs cannot be ignored.

been recorded in certain Indian squirrels and more than once in the dog.

The male measures 15 to 25 cm. in length and about 3 mm. in thickness; the female is 20 to 40 cm. long and about 5 mm. thick. The dorsal lip bears two double papillæ, each subventral lip one double papilla and two very small simple papillæ. The œsophagus is about 6.5 mm. long. In the male two pairs of the postanal papillæ are double, and there is a large, median, cushion-like structure immediately in front of the cloaca. The vulva is situated at about the anterior third of the body, frequently in an annular constriction. The eggs are oval, measuring 0.05 to 0.07×0.04 to 0.05 mm. The egg-shell is thick, and is covered before laying with an irregular coat of a viscid albuminous substance.

The main facts of the life-history of this species, which has been carefully worked out by Stewart, Ransom, Yoshida and other workers, are

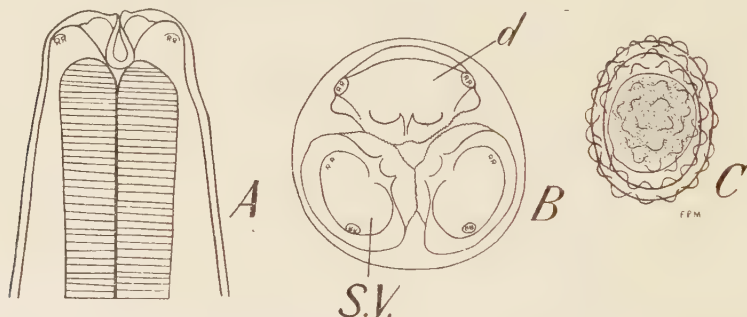


FIG. 92.—*Ascaris lumbricoides*. (AFTER YORKE AND MAPLESTONE.)

A, anterior end, ventral view; B, lips, *en face*; C, egg; d., dorsal lip; s.v., subventral lip.

briefly as follows. The eggs reach the infective stage after lying in the open for some weeks, during which period they are extremely resistant to environmental conditions and to chemical substances. They can remain alive and infective for several years. If ingested by a suitable mammal, they hatch in the small intestine, and the larvæ burrow into the wall of the intestine and penetrate into the small mesenteric veins or lymphatic vessels. Carried by the blood-stream of the portal system* they reach the liver, and are thence taken to the heart and by way of the pulmonary arteries to the lungs, where they grow and moult. In the lungs they rupture the capillaries and escape into the alveoli, and finally, by way of the bronchi and trachea, they reach the mouth and are swallowed a second time. The fourth and last moult takes place soon after the young worms reach the intestine, where they rapidly develop to maturity.

* According to Yoshida's observations, the larvæ may alternatively penetrate into the abdominal cavity and thence migrate actively into the liver.

This parasite is a frequent cause of losses among young pigs, the larvæ, when numerous, giving rise, during their passage through the lungs, to a form of pneumonia which is often rapidly fatal. The presence of the adult worms may also give rise to more or less serious digestive and other disturbances. The Ascarinæ in general may, in fact, be reckoned among the most injurious of parasites.

Ascaris equorum Goeze, 1782 (= *A. megalocephala* Cloquet, 1824) is a parasite of the horse, donkey, mule and zebra, and apparently rarely of the ox. It has about the same range of measurements as *A. lumbricoides*, though its average size is rather larger, and the female attains a greater thickness (about 8 mm.). The "head" is distinctly wider than the neck, and the lips are relatively large. Each lip has a well-marked anterior lobe separated from the broad basal portion by a deep transverse groove on the inner surface. There are slight rudiments of interlabia.* The caudal end of the male has a pair of small lateral alæ. Among the postanal papillæ there are two or three pairs with double terminations. On the anterior lip of the cloaca there is a median papilla. The vulva of the female is situated at about the anterior quarter of the body. The eggs are subglobular, with finely pitted shells measuring 0.09 to 0.1 mm. in diameter.

Ascaris vitulorum Goeze, 1782, occurs in the ox, zebu and domesticated Indian buffalo, being especially common in young calves. It has been recorded in Europe, several parts of Asia, the Philippines, Africa, the West Indies and the United States.

The male measures up to 25 cm. in length and 3 to 5 mm. in thickness; the female up to 30 cm. in length and 5 to 6 mm. in thickness. The "head" is distinctly narrower than the neck, which forms a kind of "shoulder" behind the lips. The lips are broad at the base and narrow in front. There are no interlabia. The œsophagus is 3 to 4.5 mm. long, and is modified posteriorly to form a very small "ventriculus" or granular bulb, which is not, however, distinctly constricted off.†

The tail of the male commonly forms a small, constricted-off appendage, with slight lateral alæ. There are three to five pairs of postanal papillæ, of which the most anterior pair are very large and double. The preanal papillæ are apparently very variable in number (nine to forty pairs, according to different observers). The spicules measure 0.95 to 1.25 mm. The vulva is situated at one-tenth to one-sixth of the total length from

* This species (presumably on account of the structure of the lips and the presence of small interlabia) has been placed by Yorke and Maplestone (1926) in a separate genus, *Parascaris*.

† On account of this peculiarity Travassos (1927) has proposed a new genus, *Neoscaris*, for this species.

the anterior end. The eggs have coarsely granulated shells, and measure 0.075 to 0.095×0.06 to 0.075 mm.

On account of certain discrepancies between various existing descriptions of this worm, it has been suggested that there are possibly two or more closely related species of *Ascaris* in cattle in different parts of the world. Apart, however, from the occasional occurrence of *A. lumbricoides* and *A. equorum*, it is probable that there is but a single somewhat variable species.

Two species of "*Ascaris*" from man are based on single records and are of uncertain position. These are **A. texana** Smith and Goeth, 1904,

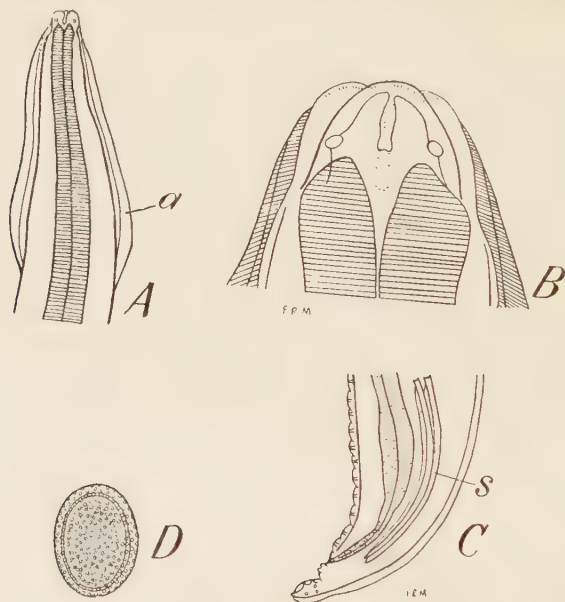


FIG. 93.—*Toxocara canis*. (AFTER YORKE AND MAPLESTONE.)

A, anterior end, ventral view; B, lips, dorsal view; C, posterior end of male, lateral view; D, egg; a., cervical ala; s., spicules.

from Texas (a worm measuring about 60 mm. in length, and said to have interlabia), and **A. maritima** Leuckart, 1876, from Greenland (an immature female worm, 43 mm. long and 1 mm. thick, without interlabia, said to have been vomited up by a child in 1865).

The Ascarids found in dogs and cats belong to two closely related genera characterized by the presence of well-developed lateral cervical alæ which give the anterior end the appearance of an arrow- or spear-head. The life-history of these forms is similar to that of *Ascaris lumbricoides*, and they are liable to have similar injurious effects, especially upon young animals. Puppies and kittens a few days old are often found to

be infested, which is explained by the fact that prenatal infection has been shown to be possible.

In **Toxocara** Stiles, 1905 (—*Belascaris* Leiper, 1907) the cervical alæ exhibit relatively coarse transverse striations, and the body is bent ventrally anteriorly. Interlabia are absent. The œsophagus has a small, distinct muscular bulb posteriorly. The tail of the male has a well-marked terminal digitiform appendage, and caudal alæ are more or less well developed. The spicules are subequal and alate. The coils of the female genital tubes extend throughout almost the whole length of the body. The eggs are subglobular, with thin, pitted shells.

Toxocara canis (Werner, 1782) (—*Belascaris marginata* (Rud., 1802) of Railliet and Henry, 1911) occurs in the dog, wolf and fox. It is a form measuring up to about 10 cm. in length in the male and up to 18 cm. in the female. The spicules are 0.75 to 0.95 mm. long. The eggs measure about 0.075 to 0.08 mm. in diameter.

Toxocara mystax (Zeder, 1800) (—*Belascaris cati* (Schränk, 1788) of some authors) is a parasite of the cat and of a number of wild members of the cat tribe, and also, accidentally, of man. In this species the cervical alæ are usually very broad, with conspicuous striations. The male is 3 to 6 cm. long, the female 4 to 10 cm. The spicules measure 1.7 to 1.9 mm. The eggs have a diameter of 0.065 to 0.075 mm.

In **Toxascaris** Leiper, 1907, the transverse striations on the cervical alæ are relatively fine, and the body is bent dorsally anteriorly. Interlabia are absent. The œsophagus has no posterior bulb. The tail of the male is conical and without a digitiform appendage or alæ. The spicules are subequal and non-alate. The coils of the female genital tubes lie only between the vulva and the posterior end of the body. The eggs are subglobular, with thick, smooth shells.

Toxascaris leonina (v. Linstow, 1902) occurs chiefly in wild Felidæ (lion, tiger, etc.), but has been observed occasionally in the domestic cat in England, and may possibly be commoner in that animal than is generally supposed. It is a relatively small and slender form, measuring 2 to 8 cm. in length. The spicules measure 0.9 to 1.25 mm., and the eggs have a diameter of about 0.07 to 0.08 mm.

Toxascaris limbata* Railliet and Henry, 1911, occurs in the dog and jackal, and has apparently also occurred in man. It measures 4 to 6 cm. in the male and 6.5 to 10 cm. in the female. The spicules are 1.2 to 1.5 mm. long, and the eggs measure 0.075 to 0.085 mm. in diameter.

The genus **Lagochilascaris** Leiper, 1909, may be characterized briefly as follows. Lateral alæ are present throughout the whole length of the

* According to Taylor (1924), this species is identical with *T. leonina*.

body. The lips are separated by a transverse groove from the neck. The free edge of each lip is deeply indented in the middle. Well-developed interlabia are present. The œsophagus is simple. The tail of the male is bluntly conical, and bears at least five pairs of postanal papillæ, of which the most anterior are large and double. There are at least twenty-four pairs of preanal papillæ. The spicules are subequal and non-alate. The vulva is in front of the middle of the body. The eggs are globular, with thick, pitted shells.

L. minor Leiper, 1909, is a form which has been found in man on several occasions in Trinidad and once in Dutch Guiana, in subcutaneous abscesses. The male measures 9×0.4 mm., the female 15×0.5 mm. The œsophagus is 1.1 to 1.2 mm. long. The spicules are 3.5 and 4 mm. long respectively, and are colourless. The vulva is situated at 6 mm. from the anterior end. The eggs are 0.065 mm. in diameter. The situations in which this worm has been found suggest, as Leiper states, that man is not the normal host, and since two other species of the genus are known, one in the lion and one in an opossum, it is probable that the alimentary canal of some carnivorous mammal is its proper habitat.

In the subfamily **Anisakinæ** the œsophagus may or may not be divided into an anterior muscular portion and a posterior ventriculus of different histological structure, or a muscular bulb. When a ventriculus is absent, and frequently when it is present, there is an anterior cæcum springing from the intestine and lying alongside of the œsophagus. A glandular appendix, or several such appendices, may be developed in connection with the ventriculus. The adult worms are parasitic chiefly in aquatic or fish-eating vertebrates. In several, if not all, of the genera an intermediate host is required, in which the larva remains encapsuled among the connective tissue until it is ingested by the final host.

The only genus of this group to be considered here is **Porrocæcum** Railliet and Henry, 1912. In this genus the lips are provided with denticulous ridges, and interlabia are usually present. The œsophagus has a posterior ventriculus, without appendix. An anterior intestinal cæcum is present. An accessory piece is present in the male only in exceptional species.

Porrocæcum crassum (Deslongchamps, 1824) occurs in the intestine of ducks, both domestic and wild, in Western Europe. The body is rather stout, tapering at each end, and measures 12 to 30 mm. in length and 0.5 to 1.2 mm. in thickness in the male, and 43 to 50 mm. and about 2 mm. respectively in the female. The ventriculus is very short and almost globular in shape. The spicules are short (about 0.6 to 0.7 mm.), and there is no accessory piece. The vulva is situated a little behind the middle of the body. The intermediate host of this species is unknown.

HETERAKIDÆ.

The family **Heterakidæ** consists of medium-sized or rather small forms in which the lips are typically well defined, though sometimes much reduced. Either a chitinous buccal capsule is present or the anterior portion of the œsophagus is differentiated as a small muscular pharynx. The posterior end of the œsophagus is almost always enlarged to form a subglobular muscular bulb containing a three-sided valvular apparatus. There is a more or less well-developed preanal sucker in the male, with or without a chitinous border, and provided with special musculature. There are usually two spicules. An accessory piece may be present or



FIG. 94.—*Heterakis gallinæ*: ANTERIOR END, DORSAL VIEW. (AFTER YORKE AND MAPLESTONE.)
a., cervical ala; b., œsophageal bulb; c.p., cervical papilla; n., nerve-ring.



FIG. 95.—*Heterakis gallinæ*: POSTERIOR END OF MALE, VENTRAL VIEW. (AFTER LANE, MODIFIED.)
cl., cloacal aperture; s., sucker.

absent. The vulva is typically near the middle of the body. The life-history is direct, without intermediate host.

In the subfamily **Heterakinæ** the lips are well defined, and there is a muscular pharynx. The preanal sucker of the male is nearly circular and has a chitinous border.

Heterakis Dujardin, 1845, is a genus containing a considerable number of rather small species (averaging about 1 cm. in length) found in the

alimentary canal of birds and mammals. The body usually has well-developed lateral alæ. The œsophagus has a well-defined posterior bulb. The male has well-developed caudal alæ, supported by about ten to fifteen pairs of pedunculate papillæ. The spicules are equal, subequal or markedly unequal in length, and sometimes dissimilar in form. There is no accessory piece. In some species papilla-like protuberances may be seen in the neighbourhood of the vulva in mature females. These are probably produced by the action of the sucker of the male. The eggs have thick shells, and their contents are unsegmented when laid.

Heterakis gallinæ (Gmelin, 1790) (= *papillosa* (Bloch, 1782), *vesicularis* (Frölich, 1791) of many authors) is a common species in nearly all parts of the world, occurring in the cæca of the fowl, turkey, guinea-fowl, pea-fowl, pheasant, duck, goose and various other birds (chiefly Galliformes). The male measures 7 to 13 mm., and the female 10 to 15 mm., in length. The œsophagus (including the bulb) measures about 1 mm. or a little more. The spicules are very unequal and dissimilar, the right spicule being slender and about 2 mm. long, the left broadly alate and only about 0.65 to 0.7 mm. long. The chitinous ring of the preanal sucker usually has a diameter of 0.06 to 0.07 mm. The vulva is a little behind the middle of the body. The eggs measure 0.063 to 0.075 × 0.036 to 0.048 mm.

Three other species of *Heterakis*, rather smaller than *H. gallinæ*, occur in the cæca of the fowl in different parts of the world. They are readily distinguished by the size and shape of the spicules of the male, as follows:

H. brevispiculum Gendre, 1911. Spicules equal, 0.4 mm. long, alate, with a barb on the dorsal side near the tip. Occurs in West Africa and Brazil.

H. beramporia Lane, 1914. Spicules subequal. 0.3 to 0.7 mm. long, the left spicule expanded distally and angulated ventrally near the tip. Occurs in India and the Philippines.

H. putaustralis Lane, 1914. Right spicule 0.55 mm., tapering to a blunt point. Left spicule 0.26 mm., with wide, asymmetrical alæ. Occurs in India.

A closely related form, **H. isolonche** v. Linstow, 1906, though not known in the fowl, not infrequently causes losses among pheasants kept in captivity. It burrows in the lining of the cæca, producing in some cases a severe inflammatory condition known as "nodular typhlitis." This species is also readily recognized by the size of the spicules, which are equal or subequal, alate, and 1.4 to 1.8 mm. long.

Heterakis dispar (Schrank, 1790) occurs in the cæca of the goose and duck. It is a larger form than *H. gallina*, the male measuring 11 to 18 mm. and the female 16 to 23 mm. or more in length. The spicules are subequal and relatively short.

The genus **Ascaridia** Dujardin, 1845, consists of larger species, on the average, than *Heterakis*. The œsophagus is simple and club-shaped, without a posterior bulb. The male has slight caudal alæ and relatively large, mainly sessile, caudal papillæ. The spicules are equal or subequal, and there is no accessory piece. There is a preanal sucker, with a circular or elliptical chitinoid ring, as in *Heterakis*. The eggs have an internal thickening of the shell at one pole. The worms occur in the small intestine of birds and reptiles.

Ascaridia perspicillum (Rudolphi, 1803) (= *A. inflexa* (Zeder, 1800) of some authors) is a common parasite of the fowl, turkey and guinea-fowl in Europe and Asia, and has also been recorded from the duck. The male is 3 to 8 cm. long and about 0.6 mm. thick. The female measures 6 to 12 cm. and 1.6 to 1.8 mm. respectively. The spicules measure about 1.1 mm. in length, and have blunt, button-like terminations. The eggs measure about 0.077×0.047 mm. This species is not uncommonly met with in the albumen of hens' eggs, the explanation of its presence being that the worm sometimes wanders from the intestine into the cloaca, whence it finds its way into the oviduct, and becomes enclosed in an egg at the time of deposition of the shell.

Ascaridia lineata (Schneider, 1866) (synonyms: *A. hamia* Lane, 1914; ? *A. brasiliensis* Magalhães, 1892) occurs in the fowl, duck and goose in Asia, Africa, North and South America and the Philippines. This is said to be the common species in poultry in the United States, and it is doubtful whether *A. perspicillum* occurs there. The length of *A. lineata* is 7 to 12 cm. The spicules measure, according to Schwartz, from 0.54 mm. in young males to 2.4 mm. in full-grown specimens.

A. compar (Schrank, 1790), which occurs in a number of wild Galliform birds, has also been recorded from the domestic fowl in the Philippines. The male measures about 3.5 to 5 cm., the female about 8 to

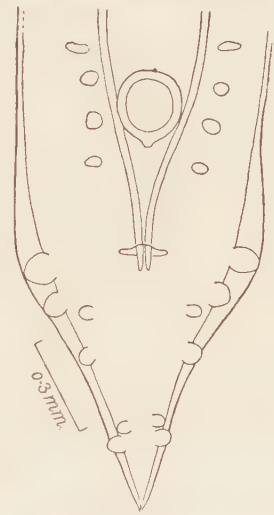


FIG. 96.—*Ascaridia perspicillum*: POSTERIOR END OF MALE. VENTRAL VIEW. (AFTER BAYLIS AND DAUBNEY.)

10 cm., in length. The spicules are about 1.8 mm. long and the eggs measure about 0.09×0.06 mm.

A. styphlocerca (Stossich, 1904) was originally described from an unnamed "domestic bird" from Gambia. It has recently been recorded by Miss Cram from the fowl in South Africa. The length of this worm is 9 to 10 cm. The œsophagus (in the male) is 3.9 mm. long. The ventral caudal area of the male, as far forward as the sucker, is covered with refringent granulations. The sucker measures 0.232 mm. in outside diameter antero-posteriorly and 0.183 mm. laterally. The spicules are at least 2.5 mm. long.

Two further species of *Ascaridia* have been described from the fowl, but are of somewhat doubtful status. These are **A. compressa** (Schneider, 1866) from Adelaide, Australia (male 53 mm., female 85 mm. long), and **A. granulosa** (v. Linstow, 1906) from Ceylon (male 27 mm., female 55 mm. long; sucker of male surrounded by granulations). The length of the spicules is not described for either of these species.

Ascaridia columbæ (Gmelin, 1790) (= *A. maculosa* (Rud., 1802)) is a widely distributed parasite of pigeons, including the domesticated breeds. It is very variable in size, the male measuring 16 to 70 mm. in length, and the female 20 to 95 mm. The spicules are 1.2 to 1.35 mm. long. The eggs measure 0.08 to 0.09×0.04 to 0.05 mm. This worm may be present in enormous numbers without, apparently, causing the bird any inconvenience.

Ascaridia anseris Schwartz, 1925, is recorded from the domestic goose in Indo-China. The male measures 32 mm. in length and 0.6 mm. in thickness. The spicules are subequal, measuring 0.82 mm. and 0.827 mm. respectively. The female has not been described.

In the subfamily **Subulurinae** the lips are much reduced or absent, and a cylindrical, chitinoid buccal capsule is present. The œsophagus is without a pharyngeal portion, but has a posterior bulb. A preanal sucker is usually present, and this is elongate and fusiform or elliptical in shape, without a chitinoid border. The eggs usually contain fully-formed embryos when laid.

In **Subulura** Molin, 1860, the typical genus, the mouth is usually oval or hexagonal, with its long axis dorso-ventral. The buccal capsule has three teeth at its base. Lateral cervical alæ are frequently present. The caudal papillæ of the male are sessile, and consist of eleven pairs or fewer. The spicules are equal, slender and alate, and an accessory piece is present, usually of triangular shape. The sucker is fusiform. The eggs are subglobular. The species occur chiefly in birds and mammals.

Subulura (Allodapa) differens (Sonsino, 1890) occurs in the intestine of the fowl and guinea-fowl in Southern Europe, Africa and Brazil. The male measures about 8.6 mm. in length and 0.28 mm. in thickness, the female 11.3 to 12.5 and 0.33 mm. respectively. The spicules are 1.016 mm. long, according to Barreto, and the eggs measure 0.059 × 0.05 mm.

S. (Allodapa) brumpti (Lopez Neyra, 1922) has been recorded from the cæca of the fowl, turkey and guinea-fowl in Spain, Africa and South America. It is very closely related to *S. suctorica* (Molin, 1860), a form which occurs in goatsuckers, and it is probable that records of the occurrence of *S. suctorica* in poultry generally refer to *S. brumpti*. This species is 6.9 to 10 mm. long in the male, 9 to 13.7 mm. in the female, and about 0.3 to 0.5 mm. in thickness. The spicules are 1.32 to 1.5 mm., and the accessory piece 0.175 to 0.21 mm., in length. The eggs measure 0.075 to 0.08 × 0.065 to 0.07 mm.

KATHLANIIDÆ.

The family **Kathlaniidæ** consists of small or medium-sized forms in which there are three well-developed lips, which may be entire or subdivided. There is either a chitinoid buccal capsule or a muscular pharynx. The œsophagus has both a posterior bulb and a prebulbar swelling. These two swellings are separated by a narrow neck, and together have the appearance of a dumbbell-shaped or flask-shaped bulb. The male is without caudal alæ, and has a number of sessile papillæ. Sucker-like preanal organs are present in some of the genera. There are two equal or subequal spicules, usually broadly alate, and usually an accessory piece. The vulva is near the middle of the body, and the uterine branches are opposed.

The only form belonging to this family with which we are here concerned is **Probstmayria vivipara** (Probstmayr, 1865) Ransom, 1907. This is a very small worm (2 to 2.9 mm. in length) found in the colon of the horse, donkey and zebra in Europe, Africa and North America. In this species the lips are bilobed, and there is a tubular pharynx, 0.04 to 0.05 mm. long, composed of a short, non-muscular anterior portion and a longer, muscular posterior portion. The male has no sucker-like organ. The spicules are subequal (0.067 and 0.058 mm. long), and there is no accessory piece. The female is viviparous, the embryos hatching in the uterus and growing almost to the size of the parent before birth. This is one of the very few cases known among Nematodes in which multiplication appears to be possible within the host. Nothing is known of the existence of a free-living stage.

OXYURIDÆ.

The forms contained in the family **Oxyuridæ** are for the most part small worms, with simple and usually inconspicuous lips, and without a buccal capsule. A pharynx is usually present, and the œsophagus always has a distinct posterior bulb. The male is usually much smaller than the

female. The females are oviparous, and have short ovaries, producing relatively few and large eggs. In this respect these worms may be regarded as primitive, and not very far removed from their free-living ancestors. The excretory pore is usually connected with a bladder-like structure, and is situated at about the level of



FIG. 97.—*Oxyuris equi*: OUTLINES OF THREE FEMALES (NATURAL SIZE) TO SHOW VARIATION IN LENGTH OF TAIL. (FROM NEUMANN, AFTER RAILLIET.)



FIG. 98.—*Oxyuris equi*: ANTERIOR END OF FEMALE, DORSAL VIEW. (AFTER YORKE AND MAPLESTONE.)

the œsophageal bulb or even behind it. The female always has a long, tapering tail. The male is, except in one genus, without a preanal sucker.

In *Oxyuris Rudolphi*, 1803, the œsophagus is relatively short and somewhat hourglass-shaped, and there is a short pharynx, containing numerous bristles in both sexes and three prominent teeth in the female. The tail of the male is truncate, with alar expansions in front of and

behind the cloaca, each supported by a pair of pedunculate papillæ. Some smaller caudal papillæ are also present. There is a single spicule, which is small and sharply pointed, and no accessory piece. The vulva is situated rather far forward, but behind the œsophagus. The common trunk of the uterus is extremely long, extending to the root of the tail, and there giving off two short branches which run forward parallel to each other. The eggs are elongate and flattened on one side, and have thick shells with an opening at one pole filled by a plug.

Oxyuris equi (Schrank, 1788) (synonyms: *O. curcula* (Rudolphi, 1803); *O. mastigodes* (Nitzsch, 1857)) is a cosmopolitan parasite of the colon and cæcum of the horse, donkey, mule and zebra. The male measures 9 to 12 mm. in length, the female 40 to 150 mm. A large proportion of the



FIG. 99.—*Oxyuris equi*: TWO VIEWS OF POSTERIOR END OF MALE.
(AFTER RAILLIET.)

s., spicule.

length of the female is taken up by the tail, which is much more slender than the body and of extremely variable length. The spicule of the male measures 0.12 to 0.165 mm.

A second species, **O. poculum**, found in the horse in Ceylon, was described by von Linstow in 1904. It appears to differ from *O. equi* in several respects, particularly in the length of the spicule (0.44 mm.).

Oxyuris compar Leidy, 1856, recorded from the small intestine of the cat in the United States, is a species of doubtful status. In any case, it probably does not belong to the genus *Oxyuris* in the restricted sense, and may be a "pseudoparasite" derived from some other animal eaten. According to Hall, Leidy's specimens were probably examples of *Passalurus* [*Oxyuris*] *ambiguus* (Rudolphi, 1819), normally a parasite of rabbits.

The species **Oxyuris incognita** Kofoid and White, 1919, was based on eggs found in human fæces. These eggs, however, have been shown by Sandground to have been probably those of *Heterodera radiculicola*, a form

parasitic on the roots of plants, which had been swallowed and passed through the alimentary canal.

In *Enterobius* Leach, in Baird, 1853, the cuticle of the anterior end forms an ovoid vesicular swelling, and narrow lateral alæ are present. The œsophagus has a prebulbar swelling and a distinct bulb. The tail of the male is truncate, with alæ supported by a pair of pedunculate pre-anal papillæ and by another pair at the posterior end. Two or three pairs of sessile postanal papillæ are also present. The single spicule is relatively long, and there is no accessory piece. The vulva is in the anterior half of the body. The common trunk of the uterus is short, and its branches are parallel.

Enterobius vermicularis (Linnæus, 1758) is a common parasite of man (especially of children) in all parts of the globe. The males and young

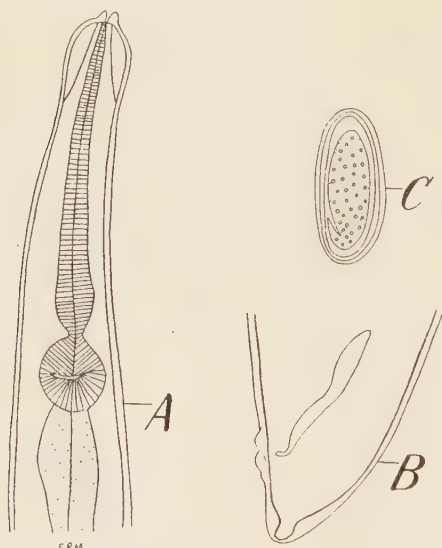


FIG. 100.—*Enterobius vermicularis*. (AFTER YORKE AND MAPLESTONE.)

A, anterior end, ventral view; B, posterior end of male, lateral view; C, egg.



FIG. 101.—*Enterobius vermicularis*: SPICULE. (AFTER BAYLIS.)

r., retractor muscle.

females inhabit the lower part of the small intestine and the large intestine, the females wandering down to the rectum when gravid. This species has also been recorded not infrequently in dogs, but the determination is open to question. The male measures 2 to 5 mm., the female 9 to 12 mm., in length. The spicule is relatively stout and has a slender, slightly recurved tip. Its total length is about 0.125 to 0.13 mm., including a solid basal portion and a tubular distal portion, 0.076 to 0.08 mm. long. The eggs measure 0.05 to 0.06 × 0.025 to 0.032 mm.,

and are slightly flattened on one side. They contain embryos which reach the infective stage soon after being laid, and owing to the habits of the female worms, which frequently escape from the anus and cause intense irritation, particularly at night, reinfection by means of soiled fingers is of very frequent occurrence.

Skrjabinema ovis (Skrjabin, 1915) Vereschagin, 1926, is a form found in the large intestine of sheep and goats in Turkestan. The male is 3.1 to 3.45 mm. in length, the female 6.8 to 7.64 mm. The buccal cavity is bounded by three trilobed lips, each having a median longitudinal ridge externally, and by three small, pointed interlabia. The cuticle of the anterior end of the body is inflated, and behind this inflation there is a pair of lateral alæ. The œsophagus has an anterior cylindrical portion and a large spherical posterior bulb. The former measures 0.34 to 0.36 mm. in length in the male, 0.54 to 0.77 mm. in the female. The diameter of the bulb is 0.07 to 0.15 mm. in the male and 0.17 to 0.24 mm. in the female. The male has a caudal alar expansion, almost circular in outline, and supported by a pair of large preanal processes bearing a number of small papillæ, and a similar but smaller pair of postanal processes. Between the preanal and postanal processes there is a pair of pedunculate papillæ. The tail has a short terminal spike. There is a single, stout spicule measuring 0.09 to 0.12 mm. in length, and an accessory piece 0.019 to 0.026 mm. long. The tail of the female is 0.9 to 1.17 mm. long. The vulva is situated at 2 to 2.24 mm. from the anterior extremity. The eggs are slightly flattened on one side and measure 0.054 to 0.057 $\times$ 0.032 to 0.034 mm.

Syphacia obvelata (Rudolphi, 1802), normally a parasite of the large intestine of rodents, including the house-mouse and black rat, has been recorded once from the faeces of a child in the Philippines. The male of this form is 1.6 mm. in length, the female 3.5 to 5.7 mm. The œsophagus has a short pharynx, a prebulbar swelling and a distinct bulb. The tail of the male ends in a long filament, at the base of which the caudal alæ terminate. There is a single relatively long spicule, measuring 0.085 mm., and an accessory piece, which is ploughshare-shaped and 0.037 mm. long. The vulva is usually prominent. The eggs are relatively very large, measuring 0.11 to 0.142 $\times$ 0.03 to 0.04 mm.

RHABDITIDÆ.

The family **Rhabditidæ** consists of small forms, many of which are free-living. Some, however, are parasitic, while others have both free-living and parasitic phases. There is a buccal cavity, usually without

teeth. The reproductive organs are of a simple and probably primitive type. The females are oviparous or viviparous. Parthenogenesis or hermaphroditism not infrequently occurs.

To this family may be referred the genus *Strongyloides* Grassi, 1879, which normally has alternating and quite dissimilar free-living and parasitic generations. These may be defined as follows:

Free-living ("Rhabditiform") Generation.—Microscopic forms, comparatively stout. Sexes separate. Mouth with four indistinct lips and

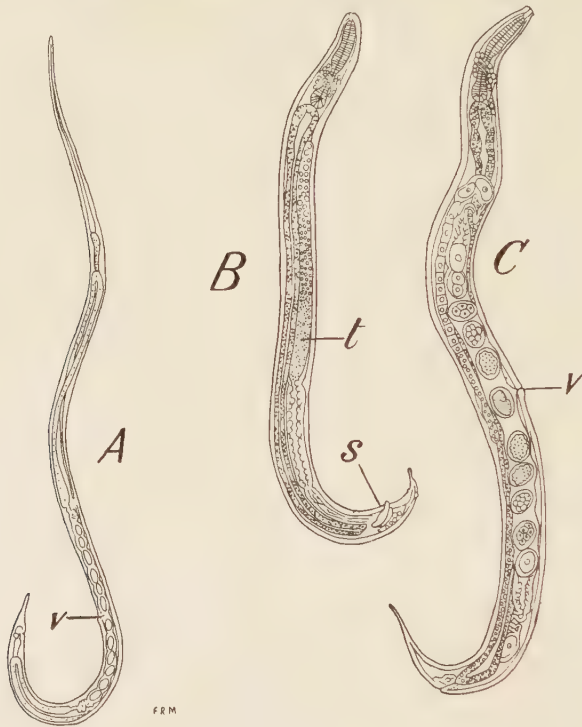


FIG. 102.—*Strongyloides stercoralis*. (AFTER LOOSS.)

A, parasitic form; B, C, male and female of free-living form; s., spicule; t., testis; v., vulva.

six papillæ. A short, cylindrical buccal capsule present. Œsophagus club-shaped, connected by a narrow neck with a pyriform posterior bulb. Tail of male short, conical. At least one pair of preanal and one pair of postanal papillæ present. Spicules short, stout, equal. An accessory piece present. Tail of female somewhat longer, tapering. Vulva near the middle of the body, opening directly into the uterine branches, which are opposed. Ovaries reflexed. Eggs few and large, oval, thin-shelled, segmenting when laid, or, in the case of older females, hatching *in utero*.

Parasitic ("Filariform") Generation.—Body considerably longer than in the free-living generation, and very slender. Consisting of "female" forms only. Mouth with four indistinct lips. A short buccal capsule present. Œsophagus long, slender, almost cylindrical, without a posterior bulb. Tail short, conical. Vulva in posterior half of body, opening directly into uterine branches, which are opposed. Ovaries reflexed. Eggs segmenting when laid.

The parasitic forms occur in the intestine of vertebrates, the free-living stages in the faeces of the hosts or in the soil. The larvæ hatching from eggs deposited by the parasitic forms may either give rise to the free-living bisexual generation, whose progeny are again of the infective (so-called "filariform") type; or they may themselves develop directly into "filariform" larvæ, the free-living adult stage being thus cut out of the life-cycle. The factors controlling the occurrence of these two alternative modes of development are not yet understood.

The infective larvæ have the power of penetrating the skin of suitable hosts, and go through a course of migration within the body somewhat similar to that of *Ascaris* (see above, p. 130) before permanently settling in the alimentary canal.

At least three species of *Strongyloides* occur in man and domestic animals. Some of the more important measurements serving to distinguish these are set out in the following table:

TABLE VII.—MEASUREMENTS (IN MILLIMETRES) OF SPECIES OF *STRONGYLOIDES* OCCURRING IN MAN AND DOMESTIC ANIMALS.

Species	..	..	..	..	<i>S. stercoralis</i> (Bavay, 1876).	<i>S. papillosus</i> (Wedl, 1856).	<i>S. westeri</i> Ihle, 1917.
Domestic Hosts	..	..	..	..	<i>Man, Dog, Cat.</i>	<i>Sheep, Goat, Ox, Pig, Rabbit.</i>	<i>Horse, Pig.</i>
<i>Parasitic form :</i>							
Length	..	..	..	..	2.2	3.5 to 6	8 to 9
Thickness	..	..	..	..	0.034	0.05 to 0.06	0.08 to 0.095
Length of œsophagus	..	..	..	..	0.6	0.65 to 0.8	1.2 to 1.5
Length of tail	..	..	..	..	0.1	0.055 to 0.07	0.12 to 0.13
Ova, length	..	..	..	..	0.05 to 0.058	0.04 to 0.06	0.04 to 0.052
Ova, width	..	..	..	..	0.03 to 0.034	0.02 to 0.025	0.032 to 0.04
<i>Free-living form :</i>							
Length, male	..	..	..	..	0.7	0.75*	—
Thickness, male	..	..	..	..	0.035	0.035	—
Length, female	..	..	..	..	1.0	1 to 1.2	—
Thickness, female	..	..	..	..	0.05	0.04	—
Length of tail, male	..	..	..	..	0.05	0.07	—
Length of tail, female	..	..	..	..	0.12	0.1	—
Length of spicules	..	..	..	..	0.038	0.035	—
Ova, length	..	..	..	..	0.07	0.065	—
Ova, width	..	..	..	..	0.045	0.03	—

* The male of *S. papillosus* is apparently seldom seen, and does not seem to have been previously described. The measurements here given are taken from a specimen examined by the writer.

A species found in calves in France has been named *S. vituli* by Brumpt (1921), but its morphology has not been described. Another form, recorded by Fülleborn from dogs in China and Japan, and apparently morphologically identical with *S. stercoralis*, is regarded as a distinct species by Brumpt (1922), who has named it *S. canis*. *S. suis* v. Linstow, 1905, a form originally recorded by Lutz in 1885 from the pig, appears to be a very doubtful species, and is probably identical with *S. papillosus*. Certain other species have been transmitted experimentally to man and various domestic animals, but these need not be considered here.

THE ORDER STRONGYLOIDEA.

The chief characteristic of the forms included in this group is the presence, in the male, of a caudal "bursa." This is a cuticular expansion more or less completely surrounding the posterior extremity, and supported by a series of "rays," which are in reality the much elongated stalks or peduncles of modified caudal papillæ. These rays have a definite number and arrangement which is recognizable throughout the group, though in certain cases the whole bursa may be much reduced and the typical arrangement of the rays somewhat obscured. In the majority of the Strongyloidea six pairs of rays and an unpaired, median, posterior or "dorsal" ray are present, and, as they are of considerable importance from the taxonomic point of view, it is necessary to indicate their general arrangement and the nomenclature here adopted in describing them. The rays fall into three divisions or systems, known respectively as dorsal, lateral and ventral. There is, as has been mentioned, a median dorsal ray which usually occupies the position of the "tail" (*i.e.*, the postanal portion of the body) in other groups of Nematodes. This may be variously branched or subdivided. At its sides, either springing from its own stem or base, or arising from the body independently of it, there is a pair of simple rays called the externo-dorsal rays. In front of the externo-dorsal ray on each side of the bursa there is a group of three rays, typically arising by the subdivision of a single large trunk, known as the lateral rays. These are termed individually, according to their positions, the postero-lateral, medio-lateral and antero-lateral* rays. In front of this group, and supporting the anterior edges of the lateral lobes of the bursa, are two more rays on each side, also typically springing from a single trunk, called the ventral, or individually the latero-ventral and ventro-ventral, rays.

The bursal membrane itself usually consists of a pair of large lateral lobes and a more or less distinct, but smaller, posterior or "dorsal" lobe.

* Also called by many authors the externo-lateral.

The mouth in the Strongyloidea is of very varying structure, but never shows the primitive three-lipped condition characteristic of the Ascaroidea. A definite chitinoid buccal capsule is frequently, but not always, present. There is reason, however, for believing that it is a primitive character of the group, since it is often present in the early larval stages even of forms in which it has disappeared in the adult. The œsophagus is simple and muscular, usually more or less club-shaped, and without a posterior bulb or ventriculus.

The spicules of the male are paired and usually equal and similar, but vary greatly in form in different families and genera. An accessory

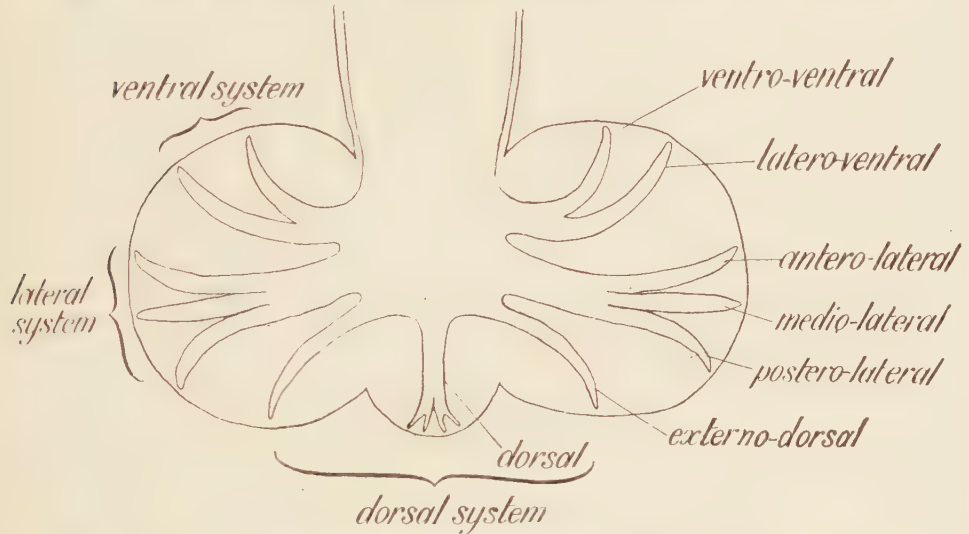


FIG. 103.—DIAGRAM OF THE BURSA OF THE STRONGYLOIDEA. (ORIGINAL.)

piece is very frequently present, and in some genera a "telamon" has also been described. The cloacal aperture is sometimes carried on a prominent structure in the centre of the bursa, known as a "genital cone." The female reproductive organs are well developed, two uterine branches being generally present. In connection with these, just before their junction with the vagina, there is frequently a pair of specialized muscular organs known as *ovjectors*. The females are usually oviparous, but occasionally ovoviviparous or viviparous. The eggs are thin-shelled and usually of relatively large size.

STRONGYLIDÆ.

In the family **Strongylidæ** there is a well-developed buccal capsule in the adults. Its anterior margin is without tooth-like structures or

cutting-plates, but is usually guarded by a circular fringe of leaf-like or bristle-like cuticular elements, collectively called the *corona radiata* or *leaf-crown*. There is frequently one such leaf-crown at the entrance to the buccal capsule and another springing from within its walls a little further back, in which case the two crowns are referred to as the external and internal leaf-crowns respectively. From the possession of these palisade-like fringes some of the Strongylidæ have received the name of "palisade-worms."

The bursa of the male is well developed in this family, and the rays depart but little, as a rule, from the typical arrangement. In some

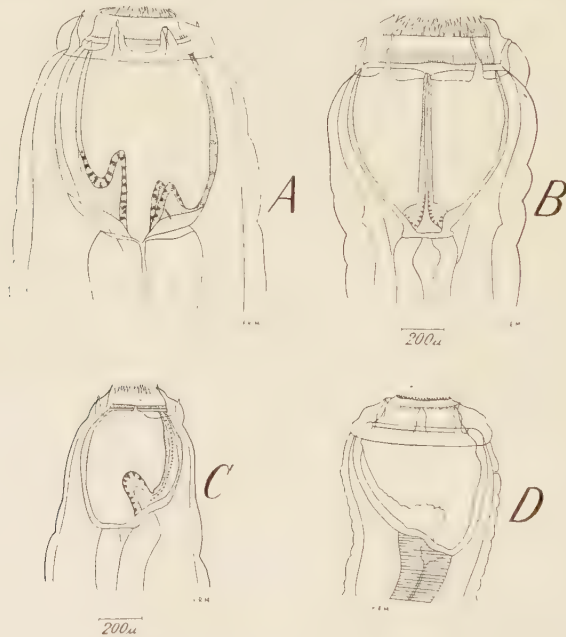


FIG. 104.—ANTERIOR ENDS OF FOUR SPECIES OF *Strongylus*
(A-C AFTER THEILER; D AFTER BOULENGER.)

(A), *S. equinus* (lateral view); (B), *S. edentatus* (dorsal view); (C), *S. vulgaris* (lateral view);
(D), *S. asini* (lateral view).

genera the dorsal lobe is exceptionally highly developed, and the dorsal ray becomes somewhat complex by the development of accessory branches.

The life-history of the Strongylidæ is always, so far as is known, a direct one, without the intervention of an intermediate host.

In the subfamily **Strongylinæ** the buccal capsule is relatively large and may be more or less subspherical or somewhat funnel-shaped. The "dorsal gutter" (a median thickening in the dorsal wall of the capsule,

carrying the terminal duct of the dorsal œsophageal gland) is usually well developed and extends nearly to the anterior margin of the capsule. The worms are parasitic in the alimentary canal of vertebrates.

In the genus *Strongylus* Müller, 1780, there is an external leaf-crown, with numerous elements, at the entrance to the mouth. The internal leaf-crown is sometimes absent. The buccal capsule is cup-shaped and thick-walled, with an external circular ridge immediately behind its anterior border. Teeth may be present towards the base of the capsule. The dorsal gutter is well developed, extending to the anterior border of the buccal capsule. The bursa of the male is relatively small and entire. The dorsal and externo-dorsal rays originate in a common trunk. Each half of the dorsal ray usually has three branches. The spicules are long, slender and unbarbed. The uterine branches are opposed. This genus includes four species found in the large intestine of animals of the horse tribe (horse, donkey, mule and zebra). These forms have been classified by Railliet (1923) in three subgenera, which may be briefly defined as follows:

Subgenus *Strongylus*. Buccal capsule with two dorsal and two sub-ventral teeth at its base. Genital cone strongly developed. Contains only the species *S. (Strongylus) equinus* Müller, 1780, of Looss, 1900.

Subgenus *Alfortia*. Buccal capsule without teeth. Genital cone well developed. Contains only *S. (Alfortia) edentatus* (Looss, 1900).

TABLE VIII.—SPECIES OF *STRONGYLUS* OCCURRING IN THE HORSE TRIBE
(MEASUREMENTS IN MILLIMETRES).

<i>Species.</i>				<i>S. equinus.</i>	<i>S. edentatus.</i>	<i>S. vulgaris.</i>	<i>S. asini.</i>
Length, male	..	..	..	26 to 35	23 to 28	14 to 16	18 to 32
Length, female	..	..	..	38 to 47	33 to 44	20 to 24	30 to 42
Thickness, male	..	..	..	1.1 to 1.3	1.3 to 1.5	0.75 to 0.95	1.8
Thickness, female	..	..	..	1.8 to 2.25	1.6 to 2.2	1 to 1.4	1.8 to 2.5
"Head"	..	..	..	Not marked off from body	Marked off by constriction, especially in female	Not marked off	Marked off by slight constriction.
Buccal capsule, shape	..	..	..	Oval	Cup - shaped, narrowing behind	Cup - shaped, more convex dorsally	Cup - shaped, more convex dorsally.
Buccal capsule, length	..	..	..	1.1	0.8 to 1.1	0.46 to 0.53	1 to 1.1
Buccal capsule, maximum width	..	..	..	0.8 to 0.9	0.8 to 1.15	0.56 to 0.6	0.94 to 1.1
Elements of external leaf-crown	..	..	..	Simple	Simple	Fringed	Simple or bifid.
Teeth	..	..	..	Conical	Absent	Rounded	Rounded or irregular.
Length of œsophagus, male	..	..	..	1.7 to 1.8	1.8	1.3 to 1.4	1.6
Length of œsophagus, female	..	..	..	2.3 to 2.5	2	1.5 to 1.7	2.4

Subgenus *Delafondia*. Buccal capsule with two dorsal teeth towards its base. Genital cone very feebly developed. Includes the species *S. (Delafondia) vulgaris* (Looss, 1900) and *S. (D.) asini* Boulenger, 1920.

These species may be further differentiated by means of the table on p. 149.

The adult worms of the genus *Strongylus* attach themselves by the mouth to the mucous membrane of the cæcum. To some extent these and other members of the family in horses are apparently blood-suckers, though they also ingest food from the contents of the lumen. Immature forms are also found in submucous nodules in the wall of the gut, from which,



FIG. 105.—*Strongylus edentatus*:
BURSA OF MALE, LATERAL VIEW.
(AFTER THEILER.)
d., dorsal ray.

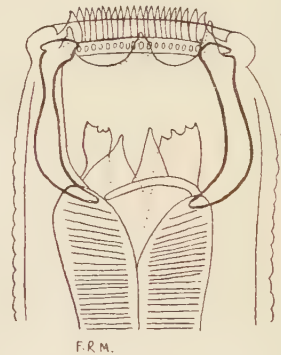


FIG. 106.—*Triodontophorus serratus*: ANTERIOR END, LATERAL VIEW. (AFTER YORKE AND MAPLESTONE.)

presumably, they escape later into the lumen. Previously to settling in the cæcum the larvæ of *S. vulgaris* undergo a course of migration by way of the blood-vessels, during which they may become lodged in the arteries, more particularly those of the mesentery, and are a frequent cause of aneurisms. This condition, with consequent intestinal congestion, sometimes leads to a fatal form of colic.

In *Triodontophorus* Looss, 1902, external and internal leaf-crowns are present, their elements being of equal number. The buccal capsule is subglobular and rather small, but has relatively thick walls. The dorsal gutter is well developed. From the œsophageal funnel three pairs of teeth project into the base of the buccal capsule. The spicules of the male terminate in small hooks. The externo-dorsal rays originate from a common trunk with the dorsal ray, and the latter is cleft almost to its

base, each half giving off two lateral branches. The vulva is relatively close to the posterior end of the body, and the uterine branches are parallel.

This genus contains at least four* species parasitic in the large intestine of members of the horse tribe. These are all of somewhat similar dimensions, ranging from about 9 to 25 mm. in length. They may be distinguished by means of the following key:

1. Median lobe of bursa short. Margins of teeth usually serrated.

(a) Vulva about 1·8 to 2·7 mm. from posterior end.

T. serratus (Looss, 1900).

(b) Vulva 0·46 to 0·56 mm. from posterior end.

T. tenuicollis Boulenger, 1916.

2. Median lobe of bursa long. Margins of teeth usually smooth.

(a) Vulva about 0·3 mm. from posterior end. Mouth-collar erect, wider anteriorly than posteriorly.

T. brevicauda Boulenger, 1916.

(b) Vulva 0·6 to 0·8 mm. from posterior end. Mouth-collar strongly depressed.....**T. minor** (Looss, 1900).

The adults of these species may cause ulceration of the colon of the host. The larvæ apparently do not undergo a course of migration outside the intestine.

The members of the genus **Craterostomum** Boulenger, 1920, also occur in the large intestine of Equidæ. This genus closely resembles *Triodontophorus*, but differs from it in having no teeth in the œsophageal funnel, in having fewer elements in the external than in the internal leaf-crown, and in having the vulva somewhat more anteriorly placed.

There are two† species, which may be distinguished as follows:

1. Elements of the external leaf-crown 6 to 8, pointed; those of the internal leaf-crown 12 to 16. Length, male, about 9·5 mm.; female, 9 to 11 mm.....**C. acuticaudatum** (Kotlán, 1919).
2. Elements of the external leaf-crown about 8, short and blunt; those of the internal leaf-crown about 24. Length, male, 6·5 to 7·25 mm.; female, 7·75 to 8·25 mm....**C. mucronatum** (Ihle, 1920).

The genus **Æsophagodontus** Railliet and Henry, 1902, contains a single species, **O. robustus** (Giles, 1892), which occurs, somewhat rarely, in the large intestine of the horse, mule and zebra. This is a form

* *T. intermedius* Sweet, 1909, has been shown by Miss Theiler to be probably a synonym of *T. serratus*, which appears to be a somewhat variable species.

† *C. tenuicauda* Boulenger, 1920, described from immature females only, is probably a synonym of *C. acuticaudatum*.

measuring 15 to 16 mm. long in the male, 19 to 22 mm. in the female. The "head" is separated from the body by a slight constriction. The buccal capsule is goblet-shaped, and is strengthened externally at its posterior end by a circular ridge. External and internal leaf-crowns are present. The mouth-collar is depressed. The lining of the œsophageal funnel is raised into three folds or teeth which do not project into the buccal capsule. A dorsal gutter is absent. The bursa of the male is without a distinct dorsal lobe, and the dorsal ray is cleft to the point of origin of its branches, which form, with the externo-dorsal rays, two groups of four rays each. The postero-lateral ray has an accessory branch springing from it posteriorly. The vulva is situated at about 2.7 to 3.7 mm. from the posterior end, and the uterine branches are parallel.

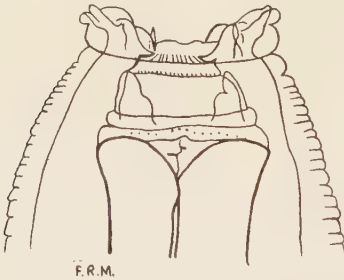


FIG. 107.—*Trichonema auriculatum*:
ANTERIOR END. (AFTER
THEILER.)



FIG. 108.—*Trichonema auriculatum*:
POSTERIOR END OF FEMALE,
LATERAL VIEW. (AFTER THEILER.)
a., anus; v., vulva.

In the subfamily **Trichoneminæ** the buccal capsule is cylindrical, with relatively thick walls. The dorsal gutter does not reach its anterior margin.

In the genus **Trichonema** Cobbold, 1874 (= *Cylicostomum* Railliet, 1901; *Cylichnostomum* Looss, 1902), external and internal leaf-crowns are present. The buccal capsule is usually rather shallow and is without teeth. The dorsal ray of the bursa is cleft almost to the point of origin of the externo-dorsal rays, and its two pairs of accessory branches spring from the bifurcate portion. The genital cone has a well-developed "dermal collar" (i.e., a granular thickening of the cuticle, especially on

its ventral surface), and usually bears appendages which may be of various shapes. The spicules are barbed at their tips. The vulva is close to the anus, and the uterine branches are parallel.

Over thirty species of this genus have been described from the large intestine of members of the horse tribe. They have been classified by various authors in a number of subgenera,* but it is a matter requiring considerable technical skill to separate many of them. Since pure infections with a single species are practically unknown, and all the species

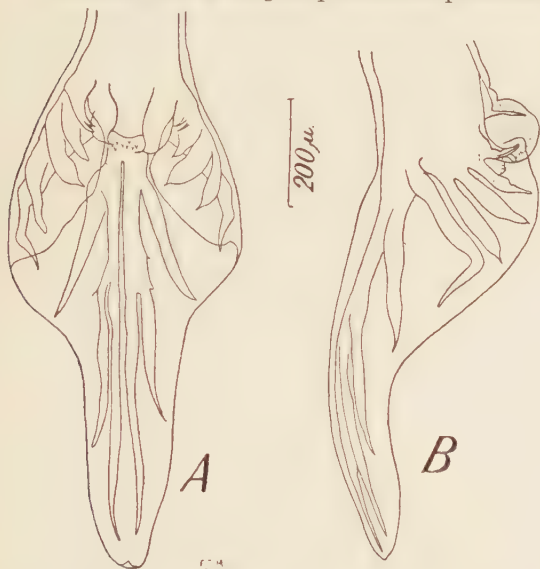


FIG. 109.—*Trichonema longibursatum*: BURSA OF MALE. (AFTER THEILER.)

A, ventral view; B, lateral view.



FIG. 110.—*Trichonema longibursatum*: PORTIONS OF MALE GENITAL ORGANS. (AFTER YORKE AND MACFIE.)

A, genital cone and appendages, lateral view; B, genital appendages, ventral view; C, tips of spicules.

presumably have similar habits and, when present in large numbers, similar pathological effects, the attempt to determine the forms present in any given infection is perhaps of somewhat academic interest. It is considered sufficient, therefore, for our present purpose to give a table (Table IX) in which certain of the more important and readily observed characters of the subgenera and species are mentioned.†

* Miss Cram (1924) prefers to regard these as genera.

† More or less well-marked "varieties" of some of the species have been described, and names have been given to them. Of these it is impossible to take account here. It should further be borne in mind that measurements alone cannot be relied upon as specific characters, owing to the large amount of variation and overlapping that occurs. Wherever possible, the various figures given by different describers have been incorporated, and it is hoped that the extreme measurements given will cover most of the variations likely to occur.

TABLE IX.—SPECIES OF *TRICHONEMA* IN THE HORSE, DONKEY, AND MULE.

Subgenus.	Species.	Length (Male) in Mm.	Length (Female) in Mm.	Buccal Capsule (Length in μ).	Buccal Capsule (Maximum Width in μ).	Number of Elements in External Leaf- Crown.	Esophagus (Length in Mm.).
<i>Trichonema</i> Le Roux, 1924 (= <i>Cylicostephanus</i> Ihle, 1922): Buccal capsule usually rather long and cylindrical, or somewhat narrowed anteriorly. Elements of internal leaf-crown short rods, originating near anterior margin of capsule. Tail of female usually straight.	<i>longicaudatum</i> (Yorke and Macfie, 1918)	5 to 7	5 to 7	17.5 to 24	26 to 32	14 to 18	0.24 to 0.34
	<i>catenatum</i> (Looss, 1900) ..	5.5 to 6.5	6.5 to 8	28 to 40	24 to 38	8 to 10	0.29 to 0.4
	<i>barbatum</i> Smit and Notosoediro, 1923 ..	8	10.5	37 to 49.5	33 to 36.3	12 to 14	0.265 to 0.352
	<i>hybridum</i> (Kotlán, 1920) ..	9 to 9.5	10 to 10.5	32	54	14 to 16	0.44
	<i>minutum</i> (Yorke and Macfie, 1918) ..	4 to 5.75	4.1 to 6	20 to 28	20	8	0.277 to 0.34
<i>Cylicostomum</i> Ihle, 1922: Buccal capsule rather short, thick-walled. Elements of internal leaf-crown triangular plates, originating some distance behind anterior margin of capsule. Tail of female straight or slightly bent dorsally.	<i>poculatum</i> (Looss, 1900) ..	8 to 9	10 to 11	60 to 82	56 to 60	30 to 35	0.77 to 1
	<i>egyptiacum</i> Railliet, 1923 (= <i>tetracanthum</i> Mehlis, of Looss, 1900)	7 to 9	8 to 12	12	60	About 22	0.36 to 0.4
	<i>coronatum</i> (Looss, 1900) ..	7 to 9	9 to 10	37 to 50	24 to 28	About 22	0.38 to 0.46
	<i>labiatum</i> (Looss, 1901) ..	7.7 to 9	9.5 to 11	12 to 16	50 to 56	About 19	0.36 to 0.38
	<i>ornatum</i> (Kotlán, 1919) ..	6.5 to 8	7.5 to 9.5	14 to 27	40 to 44	About 18	0.34 to 0.39
<i>Cylicocylus</i> Ihle, 1922: Buccal capsule with a hoop-like thickening round its posterior margin. Elements of internal leaf-crown usually fine rods, originating near anterior margin of capsule. Tail of female usually straight or only slightly bent dorsally.	<i>sagittatum</i> (Kotlán, 1920) ..	8 to 9	10 to 11	30	57	20 to 24	0.44 to 0.53
	<i>radiatum</i> (Looss, 1900)	10 to 11	12 to 12.5	40	100 to 120	18 to 20	0.6 to 0.7
	<i>adversi</i> (Boulenger, 1920)	10 to 11	11.5 to 14	52	112	26	0.8 to 1
	<i>auriculatum</i> (Looss, 1900)	12.5 to 14	14 to 16	60 to 72	140 to 160	26 to 30	0.6 to 0.72
	<i>elongatum</i> (Looss, 1900)	15 to 17	Up to 26	64 to 75	160	About 42	0.95 to 1.15
<i>Leptostomum</i> (Kotlán, 1920): <i>Leptostomum</i> (Looss, 1900) .. <i>triramoseum</i> (Yorke and Macfie, 1920) ..	<i>insigne</i> (Boulenger, 1917)	12 to 13	Up to 17	—	52	36 or more	Up to 1.4
	<i>leptostomum</i> (Kotlán, 1920)	11 to 12.5	13.5 to 15	46 to 66	130 to 200	32 to 48	0.7 to 1
	<i>nassutum</i> (Looss, 1906) ..	6	7 to 8	25 to 27	54 to 57	20 to 24	0.52 to 0.65
	<i>triramoseum</i> (Yorke and Macfie, 1920) ..	7 to 10	9 to 14	36 to 40	80	About 20	0.48 to 0.6
	<i>triramoseum</i> (Yorke and Macfie, 1920) ..	12.3	12.3 to 14	38	Over 90	At least 30	0.84 to 0.94

<i>Cylicocercus</i> Ihle, 1922:									
Elements of internal leaf-crown tri- <i>alveatum</i> (Looss, 1900) ..	..	10 to 10.5	10.5 to 13	48 to 54	—	About 29	0.6	to 0.8	
angular plates, sometimes originating at <i>caimatum</i> (Looss, 1900) ..	..	5.2 to 9	6.1 to 12	—	—	20 to 22	—	—	
a great distance from anterior margin <i>goldi</i> (Boulenger, 1917) ..	..	5.2 to 7.5	6 to 9.75	29 to 32	45 to 60	20 to 22	0.3	to 0.5	
of capsule. Posterior end of female <i>pateratum</i> (Yorke and Macfie, 1919) ..	..	8 to 11	8.4 to 15	25 to 28	85 to 89	20 to 25	0.53	to 0.76	
strongly bent dorsally, and shaped somewhat like a human foot.									
<i>Cylicodontophorus</i> Ihle, 1922:									
Buccal capsule short and wide, thick- <i>bicoronatum</i> (Looss, 1900) ..	..	10 to 12	12 to 14	17 to 24	68 to 72	30 to 34	0.6	to 0.68	
walled. Elements of internal leaf-crown <i>euproctus</i> (Boulenger, 1917) ..	..	6.75 to 8	6 to 9.5	14 to 40	64 to 100	About 40	0.36	to 0.41	
broad plates, originating fairly near <i>metami</i> (Leiper, 1913) (<i>-ihlei</i> Kotlán, anterior margin of capsule. Tail of 1921)	..	9 to 10	12 to 14	50 to 67	140 to 160	About 60	0.53	to 0.76	
female usually straight.	..	11 to 12.5	11 to 19	53 to 61	170 to 190	10 to 12	0.69	to 0.8	
<i>Cylicotetrapedon</i> Ihle, 1925:									
Walls of buccal capsule thicker in <i>asymetricum</i> (Theiler, 1923) ..	..	7.5 to 8	7.5 to 8	24 ventrally	50 to 60	About 15	0.44	to 0.5	
front than behind, and longer ventrally than dorsally. Elements of internal leaf-crown broad and short, originating near anterior margin of capsule. Tail of female straight.	..	7.5	9.5	33 ventrally	60	About 16	0.41	to 0.53	
				21 dorsally					
<i>Cylicobrachytus</i> Cram, 1924:									
Buccal capsule extremely short. <i>prioides</i> (Kotlán, 1921) ..	..	—	10 to 10.5	13 to 14	90 to 100	24 to 26	0.8	to 0.935	
Elements of internal leaf-crown in- <i>brevicausulatum</i> (Ihle, 1920) ..	..	9 to 11.5	10 to 13.5	18	110	42 to 45	0.45	to 0.635	
conspicuous or absent. Tail of female straight.									
<i>Cylicotoichus</i> Cram, 1924:									
Walls of buccal capsule much longer dorsally and ventrally than laterally. Tail of female very short and finely pointed.	..	4.3 to 6	4.5 to 6.5	32 dorsally and ventrally	—	About 18	0.33		
				22 laterally					

The life-history of the species of *Trichonema* does not, so far as is known, involve a course of migration outside the intestine of the host. Immature forms are not infrequently found in submucous cysts in the intestinal wall, from which, presumably, they escape later into the lumen.

Poteriostomum Quiel, 1919, is very closely related to *Trichonema*. The elements of the external leaf-crown are small and numerous, those of the internal leaf-crown broad and relatively few. The postero-lateral ray of the bursa gives off a short accessory branch posteriorly. The externo-dorsal ray and the two accessory branches of the dorsal ray leave the main stem above the point of its bifurcation, and are almost at right angles to it. The tail of the female is relatively long and straight. Two species of this genus occur in the horse family. They may be distinguished as follows:

1. Length, male 11 to 14 mm., female 13 to 21 mm. Œsophagus 0.63 to 0.8 mm. long. Six of the elements of the internal leaf-crown much longer than the others.

P. imparidentatum Quiel, 1919.

2. Length, male 9 to 14 mm., female 14 to 21 mm. Œsophagus 0.82 to 0.93 mm. long. Elements of internal leaf-crown all of equal length.....**P. rátzii** (Kotlán, 1919).

In **Gyalocephalus** Looss, 1900, external and internal leaf-crowns are present. The buccal capsule proper is short and thick-walled, but its walls are continuous posteriorly with thin triangular plates which form a chitinoid lining to the very large Œsophageal funnel. Three wedge-shaped tooth-like structures project from the funnel into the buccal capsule. A dorsal gutter is absent. The prebursal papillæ are very long and resemble an extra pair of bursal rays. The dorsal ray is cleft almost to the point of origin of the externo-dorsal rays, and each portion gives rise to two accessory branches.

G. capitatus Looss, 1900, a comparatively rare species occurring in the cæcum and colon of the horse, donkey and mule, measures 7 to 8.5 mm. in length in the male, and 8.5 to 11 mm. in the female. The Œsophagus is 0.86 to 1.2 mm. long. The male has a long, retractile genital cone. The tail of the female is straight and measures 0.2 to 0.3 mm. in length. The vulva is about 0.3 to 0.45 mm. in front of the anus, and the eggs measure 0.116 to 0.12 × 0.048 to 0.056 mm. A form described by Yorke and Macfie (1918) under the name of *G. equi* is considered by Ihle and by Miss Theiler to be identical with *G. capitatus*. It was held to differ from this species in the greater length of the genital cone of the male, but this appears to be a character subject to great variation.

The genus **Bourgelatia** is represented by a single species, **B. diducta** Railliet, Henry and Bauche, 1919, recorded from the cæcum and colon of the pig in Indo-China. In this form the external leaf-crown contains about twenty large, pointed elements, the internal leaf-crown about forty elements. The buccal capsule is shallow and cylindrical, and its wall is divided into two thick portions, of which the posterior is more or less continuous with the cuticular lining of a wide, shallow, œsophageal funnel. The œsophagus is 0.65 to 0.85 mm. long. The edges of the bursa are incised near the tips of the ventral rays, giving the appearance of a pair of additional lobes. The externo-dorsal rays originate high up on the main dorsal stem, and the dorsal ray is cleft for almost half its length, each portion giving off a single accessory branch. There are two alate spicules, measuring 1.25 to 1.33 mm. in length, and an ill-defined accessory piece. The male is 9.3 to 12.5 mm. long, the female 11 to 13.5 mm. The tail of the latter measures about 0.4 mm., and the vulva is situated at 0.95 to 1 mm. from the posterior end. The eggs measure 0.069 to 0.077×0.038 to 0.042 mm.

In the subfamily **Æsophagostominæ** the buccal capsule may be cylindrical or large and subglobular. A transverse ventral cervical groove is present. The cuticle of the anterior end may be dilated to form a cephalic vesicle, which is limited behind, on the ventral side, by the cervical groove.

In the genus **Æsophagostomum** Molin, 1861, a cephalic cuticular vesicle is usually present, and the ventral cervical groove extends for a varying distance on to the lateral surfaces of the worm. The lateral cervical alæ, when present, originate at the level of this groove. External and internal leaf-crowns are usually present, the latter generally containing twice as many elements as the former. The œsophageal funnel occasionally contains three teeth. The externo-dorsal rays originate high up on the dorsal stem, which is bifurcate in its posterior two-fifths. From each of the main branches arises a small accessory branch, and sometimes a second minute and slender branch. An accessory piece is present. The vulva is near the anus, and the uterine branches are parallel. This genus includes some nine species parasitic in the large intestine of domestic animals and man. These may be distinguished by means of the following table:

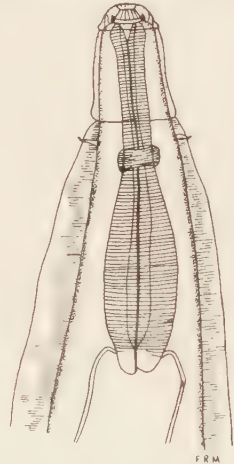


FIG. 111.—*Æsophagostomum columbianum*: ANTERIOR END, DORSAL VIEW. (AFTER RANSOM.)

TABLE X.—SPECIES OF *ÆSOPHAGOSTOMUM* IN DOMESTIC ANIMALS AND MAN (MEASUREMENTS IN MILLIMETRES).

Species.	Length (Male).	Length (Female).	Form of Mouth- Collar.	External Leaf-Crown (Number of Elements).	Internal Leaf-Crown (Number of Elements).	Position of Cervical Papillæ.	Length of Spicules.	Length of Tail (Female).	Hosts.
<i>Æsophagostomum</i> : <i>dentatum</i> (Rudolphi, 1803)	8 to 10	11 to 14	Rounded	9	18	Towards pos- terior end of œsophagus	1.15 to 1.3	0.35	Pig.
<i>longicaudum</i> Goodey, 1925	—	—	Rounded	9	18	Behind middle of œsophagus	0.91 to 0.95	0.46 to 0.47	Pig.
<i>apiostomum</i> Willach, 1891	10 to 12.8	11.5 to 16	Rounded	10 to 13	Apparently absent	—	1.25 to 1.35	0.18 to 0.21	Man, monkeys.
<i>brumpti</i> Railliet and Henry, 1905	6.7 to 11	8.5 to 12.5	Rounded	10	Apparently absent	Behind middle of œsophagus	0.9 to 1.08	0.17 to 0.2	Man, monkeys.
<i>stephanostomum</i> Stossich, 1904 (var. <i>thomasi</i> Railliet and Henry, 1909)	17 to 22	16 to 20	Rounded	38	76	About middle of œsophagus	1.38 to 1.475	0.23	Man.
<i>columbianum</i> (Curtice, 1890)	12 to 16	14 to 18	Truncate, conical	20 to 24	40 to 48	In front of middle of œsophagus	0.75 to 0.85	0.3 to 0.6	Sheep, goat, ? ox.
<i>venulosum</i> (Rudolphi, 1809)	11 to 16	13 to 24	Truncate, conical	18	36	B e h i n d œsophagus	1.1 to 1.5	0.15 to 0.2	Goat, sheep, deer, camel.
<i>asperum</i> Railliet and Henry, 1913	11 to 13	14 to 17.5	Truncate, conical	12	24	B e h i n d œsophagus	1.5 to 1.7	0.14 to 0.17	Goat.
<i>radiatum</i> (Rudolphi, 1803)	14 to 17	16 to 22	Prominent, circular in section	Absent	38 to 40	About middle of œsophagus	0.7 to 0.8	0.3 to 0.4	Ox.

It is perhaps somewhat doubtful whether a specific distinction between *O. apiostomum* and *O. brumpti* is justifiable. The human specimens described by Railliet and Henry as *O. brumpti* were immature females, but these authors assign to the same species mature specimens obtained from various monkeys. *O. stephanostomum* Stossich was originally described from the gorilla in Africa. The form named *O. stephanostomum* var. *thomasi* by Railliet and Henry was found in nodules of the wall of the intestine of a man in Brazil.

O. radiatum differs from all the other species mentioned in the form of the cervical groove, which, instead of disappearing on the dorsal side, is here continuous right round the body, and extends further back on the dorsal and ventral than on the lateral surfaces.

The earlier stages of development in this genus are spent in nodules in the intestinal wall, the worms subsequently escaping into the lumen. In the case of *O. columbianum* the nodules are found chiefly in the cæcum of the host, but in *O. radiatum* they are usually in the small intestine.

The genus **Ternidens** Railliet and Henry, 1909, which is closely related to *Æsophagostomum*, contains a single species, **T. deminutus** (Railliet and Henry, 1905), found in the large intestine of man, the gorilla and certain African and Asiatic monkeys. As a human parasite it has been recorded only from Africa. The male of this species measures 9.5 mm., and the female 11.7 to 16 mm. in length. A ventral cervical groove is present, but there is no cephalic vesicle. The external and internal leaf-crowns consist of twenty-two to twenty-four elements each. The mouth opens somewhat obliquely towards the dorsal side. The buccal capsule is subglobular, and three prominent, bifid teeth project into it from the œsophageal funnel. The spicules of the male are 0.9 mm. long. The tail of the female measures 0.27 mm. in length, and the vulva is rather prominent and situated at about 0.7 mm. from the posterior end. The eggs measure 0.06 to 0.065×0.038 to 0.04 mm.

Chabertia Railliet and Henry, 1909, also contains a single species, **C. ovina** (Gmelin, 1790). This is a parasite of the large intestine of the ox, sheep, goat and a number of other ruminants. The anterior extremity of the worm is obliquely truncate, the mouth facing antero-



FIG. 112. — *Chabertia ovina*: ANTERIOR END, LATERAL VIEW. (AFTER RANSOM.)

ventrally. There is a faint ventral cervical groove, preceded by a slight indication of a cephalic vesicle. The two leaf-crowns consist of numerous but very small elements. The length of the male is 13 to 14 mm., that of the female 17 to 20 mm. The œsophagus measures 1.2 to 1.4 mm. in length. The spicules of the male are slender and tubular, and 1.3 to 1.7 mm. long. There is an accessory piece, measuring 0.08 to 0.1 mm. in length. The tail of the female measures 0.2 to 0.23 mm., and the vulva is situated at 0.37 to 0.45 mm. from the posterior end. The eggs measure 0.09 to 0.1 $\times$ 0.05 mm., and their contents are segmenting when they are laid.

The subfamily **Stephanurinae** contains a single genus and species, **Stephanurus dentatus** Diesing, 1839 (the "kidney-worm" of swine), which is remarkable in many ways. This worm occurs in the fat surrounding the kidneys, sometimes in the liver or other abdominal viscera, or occasionally in the lungs, of the pig, and rarely in the liver of the

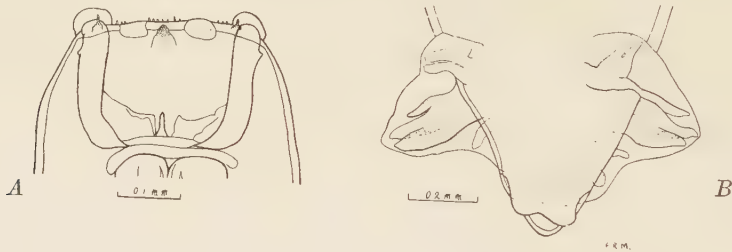


FIG. 113.—*Stephanurus dentatus*. (AFTER DAUBNEY.)

A, anterior end; B, posterior end of male, ventral view.

ox. It is a relatively stout form, measuring 20 to 28 mm. in length and up to 1.2 mm. in thickness in the male, and 25 to 45 mm. and up to 1.8 mm. respectively in the female. The buccal capsule is cup-shaped and thick-walled, and has a leaf-crown consisting of about fifty small elements at its margin, and six bicuspid or tricuspid teeth at its base. The cuticle surrounding the mouth is reflected externally to form six epaulette-like thickenings. The intestine is convoluted. The bursa of the male is poorly developed, and its rays short and stunted. The dorsal ray divides into two branches with bi- or tridigitate terminations. The spicules may be equal or unequal, and show considerable variation in different individuals. They vary from 0.66 to 1 mm. in length. When they are unequal the left spicule is the longer. There is a heart-shaped accessory piece measuring about 0.075 mm. in length. The tail of the female measures about 0.59 mm. The vulva is situated fairly close to the anus, and the uterine branches are parallel. The eggs measure 0.09 to 0.1 $\times$ 0.056 to 0.065 mm.

According to the observations of Bernard and Bauche the infective larvæ of this worm may enter the body either by penetrating the skin or by way of the mouth. In the former case they reach the perirenal fat, kidneys and ureters; in the latter case the liver.

In the subfamily **Syngaminæ** the buccal capsule is well developed and cup-shaped or subglobular, without leaf-crowns at its margin but with a number of teeth at its base. The eggs are provided with opercula. This group contains two genera parasitic in the respiratory tract of birds and mammals.

In the genus **Syngamus** v. Siebold, 1836, the adult male is much smaller than the female, and the sexes, pairing at an early age, remain permanently *in copula*, the eggs of the female escaping under the edge of the bursa of the male. The buccal capsule is large and contains eight or nine teeth at its base. The bursa of the male is thick-walled, and its rays are very short and stout. The spicules are relatively minute. The vulva is situated in the anterior third of the body in gravid



FIG. 114.—*Syngamus trachea*:
OUTLINES OF TWO PAIRS OF
WORMS. (AFTER CHAPIN.)

On the right, female immature;
on the left, female gravid.

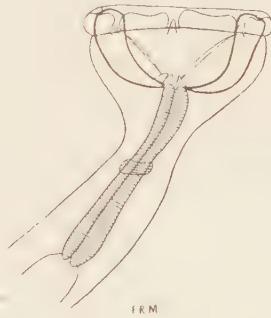


FIG. 115.—*Syngamus trachea*:
ANTERIOR END. (AFTER
YORKE AND MAPLESTONE.)

females, the postvulvar portion of the body growing considerably with the development of eggs in the uterus. Owing to their blood-sucking habits, the worms are bright red in colour when fresh.

Syngamus trachea (Montagu, 1811) (= *trachealis* v. Siebold, 1836) is a parasite of the turkey, fowl, goose, pheasant and various wild birds.

Turkeys are apparently susceptible of infection at any age, but in other birds it is usually only the young chicks that are attacked. Young chickens and hand-reared pheasants often suffer severely from the effects of the presence of this worm, which produces in them the well-known condition called "gapes," due to the accumulation of masses of the worms, enveloped in mucus and blood, in the trachea.

The male of *S. trachea* measures 2 to 6 mm. in length, the female 5 to 40 mm. The buccal capsule contains six to ten teeth (typically eight—one large dorsal tooth, two small subdorsal, two large lateral, two large subventral and one small ventral). The two terminal branches of the dorsal ray of the male are typically tridigitate, but the mode of branching is subject to considerable variation. The spicules measure 0.053 to 0.082 mm. in length. In the gravid female the coils of the uterus and ovaries lie almost entirely behind the vulva, and extend almost to the posterior end. The eggs measure about 0.085×0.05 mm.

The eggs of this worm are in process of segmentation when laid. They pass out of the host mainly by way of the alimentary canal and the droppings. The larvæ develop to the infective stage and hatch in about a week on the ground if the temperature is sufficiently high. If ingested by a suitable host, they migrate (by what route is at present unknown) to the lungs, where the young worms copulate after a few days and wander up the bronchi to the trachea. Here they become sexually mature in another ten to fourteen days. Although no intermediate host is necessary, it was observed by Walker in 1886 that earthworms were capable of acting as vectors of this worm, chicks becoming infected by eating worms which had swallowed larvæ contained in the soil.

Syngamus laryngeus Railliet, 1899, occurs in the larynx of the ox and buffalo in India, the Malay region and South America. It has been recorded once as a parasite of man in Brazil, but the determination of the species is somewhat doubtful. The male worm measures 2.6 to 5 mm. in length, the female 7 to 20 mm. The eight teeth of the buccal capsule are of approximately equal size, and the walls of the capsule are strengthened internally by six longitudinal rib-like thickenings. The dorsal ray of the bursa is apparently undivided. The spicules measure 0.025 to 0.03 mm. in length. The coils of the uterine and ovarian tubes in the female extend back only a little beyond the middle of the body, and forward to almost the same distance in front of the vulva.

S. nasicola v. Linstow, 1899, is possibly identical with *S. laryngeus*. It has been recorded from the nasal cavities of goats and deer in Brazil, Africa and Turkestan. The male is described as 5.6 mm. long, the female 20.6 mm., and the eggs as measuring 0.088×0.046 mm.

S. kingi Leiper, 1913, is a form stated to have been coughed up by a woman in St. Lucia, West Indies. No measurements are given in Leiper's description. According to some authors it is doubtful whether the species is distinct from *S. dispar* (Diesing, 1851), a form originally described from the puma in Brazil, to which Leiper states it approaches more nearly than to any other species.

In *Cyathostoma* E. Blanchard, 1849, the sexes are not permanently *in copula*. The buccal capsule is large and cup-shaped, and has six or seven teeth at its base. The bursa is normally developed, and the dorsal ray is cleft for about one-third of its length. The spicules are long and filiform, and an accessory piece may be present. The worms occur in the respiratory tract of birds.

Cyathostoma bronchialis (Muehlig, 1884) is a parasite of the goose and swan, occurring in the trachea and bronchi. Its presence occasionally causes losses among young geese. The male measures 4 to 5.8 mm., the female 16 to 31 mm., in length. The spicules are alate and 0.51 to 0.62 mm. long. The terminal branches of the dorsal ray are short, widely divergent and irregular in outline. The eggs measure 0.074 to 0.083 × 0.049 to 0.062 mm.

ANCYLOSTOMIDÆ.

The family *Ancylostomidæ* (the hookworms) contains about fifteen genera characterized by the possession of a well-developed, somewhat funnel-shaped buccal capsule armed at its anterior margin with ventral teeth or cutting-plates, and without leaf-crowns. The head is commonly bent dorsally. The accessory branches of the dorsal ray of the male are much reduced.

The life-history of all the hookworms, so far as is known, is similar. The eggs laid by the females and passed out with the host's faeces are in the early stages of segmentation. After about two days in the open, if the temperature and other conditions are suitable, the embryos develop and hatch. They now grow rapidly and moult twice, the cuticle, however, not being shed after the second moult, but remaining as a loose protective sheath. This, the infective, stage is reached in about five days or a week. Should the larvæ at this stage come in contact with the skin of a suitable host, or be taken into the mouth, they actively penetrate the skin or the mucous membrane and find their way into the lymphatic vessels or veins, and are thus carried by the blood-stream to the heart and thence to the lungs. From this point the course of their migration is similar to that of *Ascaris* (see above, p. 130). The ultimate habitat, the small intestine, is reached in seven to ten days after the larvæ enter the skin. Here, in

the course of a further two to four weeks, the worms moult again twice and become sexually mature.

In the subfamily **Ancylostominae** the main armature of the buccal capsule takes the form of one to four pairs of marginal teeth.

In **Ancylostoma** (Dubini, 1843) Creplin, 1845, the anterior end is bent dorsally, and the mouth-opening is armed with one to three pairs of ventral teeth. The buccal capsule is deep, and is provided internally with two triangular dorsal teeth. The dorsal gutter opens in a deep notch on its anterior margin. The bursa of the male has a small dorsal lobe. The externo-dorsal rays originate high up on the main dorsal stem, and the latter is cleft for about one-third of its length. There are two very short accessory branches near the tip of each main branch. There are two simple spicules and an accessory piece. The vulva is behind the middle of the body, and the uterine branches are opposed.

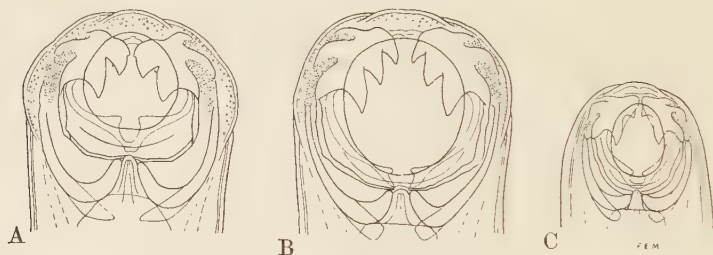


FIG. 116.—DORSAL VIEWS OF THE MOUTH OF (A), *Ancylostoma duodenale*; (B), *A. caninum*; (C), *A. braziliense*. (AFTER LOOSS.)

Three species of *Ancylostoma* occur in man and domestic animals. They are all of somewhat similar size, ranging from 8 to 10 mm. in length in the male and from 9 to 14 mm. in the female. They may be readily recognized by means of the following characters:

1. Two pairs of large ventral teeth and a rudimentary inner pair.
Length of œsophagus about 1.3 mm. Length of spicules 2 mm.
A. duodenale Dubini, 1843.
2. One pair of large ventral teeth and a rudimentary inner pair.
Length of œsophagus about 0.75 mm. Length of spicules 0.8 mm....**A. braziliense** Gomez de Faria, 1910 (= *ceylanicum* Looss, 1911).
3. Three pairs of large ventral teeth. Length of œsophagus about 1.1 mm. Length of spicules 0.9 mm....**A. caninum** Ercolani, 1859.

A. duodenale and *A. braziliense* are of practically world-wide distribution in tropical and subtropical countries, and both occur in man, as

well as in carnivorous mammals. *A. braziliense* is common in dogs and cats, while *A. duodenale*, which apparently may occur normally in certain wild carnivores, such as the tiger in India, has been experimentally transmitted to young dogs and cats, but is not, as a rule, found in older individuals. It has been recorded from the pig. *A. caninum*, which is a common and widely distributed parasite of dogs, occurs very rarely in man.

All these species are parasites of the small intestine of their hosts, and, owing chiefly to their blood-sucking and tissue-destroying habits, are among the most important of economic pests. They cause, at least when present in numbers, more or less severe symptoms of anæmia and debility, producing in man the condition formerly known as "miners' anæmia" (so called from the fact that it was early noticed that in certain underground workings even in temperate countries the conditions favoured infection); while "kennel anæmia" is an epidemic disease, due to infection with *A. caninum* or *Uncinaria stenocephala* (see below, p. 170), not infrequent among packs of hounds.

Agriostomum vryburgi Railliet, 1902, the only known species of its genus, is a parasite of the zebu in Sumatra and India. It occurs in the duodenum. In this form the mouth-opening is surrounded by a chitinous thickening from which spring four pairs of large teeth. In front of these there may be indications of a rudimentary leaf-crown. There is a ventral cervical groove, as in the *Œsophagostomina*. The buccal capsule is short, but the œsophageal funnel is very large.

The dorsal gutter ends in a bifid cone which projects freely from the buccal capsule. The œsophagus is 1 to 1.15 mm. long. The antero-lateral ray of the bursa is thicker than, and somewhat divergent from, the other lateral rays. The dorsal ray is cleft for about one-third of its length, and its terminations are bidigitate.

The male measures 9.2 to 11 mm. in length, the female 13.5 to 15.5 mm. The spicules are 0.83 to 0.87 mm. long, alate and transversely striated. An accessory piece is present. The tail of the female is 0.15 to 0.26 mm. long, and the vulva, which is prominent, is situated at 0.47 to 0.6 mm. from the posterior end. The eggs measure 0.125 to 0.195 × 0.06 to 0.092 mm.

In the subfamily *Necatorina* the anterior margin of the buccal capsule usually bears ventral cutting-plates or "semilunes," but is not provided with teeth.

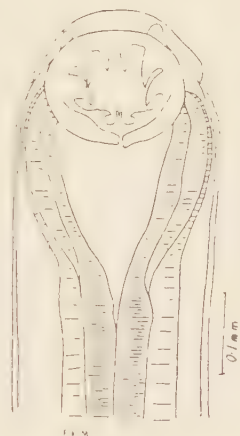


FIG. 117.—*Agriostomum vryburgi*: ANTERIOR END, DORSAL VIEW. (AFTER WARE.)

In the genus *Necator* Stiles, 1903, the anterior end is bent dorsally. There is a pair of cutting-plates on the ventral side of the mouth-opening. The buccal capsule is large and funnel-shaped. At its base are a pair of ventral lancets, a pair of subdorsal teeth and a prominent dorsal cone (the termination of the dorsal gutter) which projects freely into the lumen. The bursa has two large lateral lobes and a small dorsal lobe. The externo-dorsal rays are rather long and slender, and arise high up on the main dorsal stem. The dorsal ray is cleft for almost half its length, and its terminations are bidigitate. The spicules are slender, and their tips, which are fused, form a membranous barb shaped somewhat like one half of a spear-head. The vulva is somewhat in front of the middle of the body, and the uterine branches are opposed.

Necator americanus (Stiles, 1902) occurs in the small intestine of man, the pig, and the rhinoceros. It has also been recorded from the gorilla and (rarely) from the dog. This is the common hookworm of America. It occurs, however, in almost all tropical and subtropical parts of the world, and there is reason to believe that it was originally imported into America from Africa.

The male measures 5 to 10 mm. in length, the female 7 to 13.5 mm. The length of the œsophagus is about 0.5 to 0.8 mm. The spicules measure, as a rule, from 0.9 to a little over 1 mm., but appear to be subject to a good deal of variation in length. The eggs measure $0.053 \times 0.066 \times 0.028$ to 0.044 mm.

A form found in pigs in Trinidad has been described as a distinct species, *Necator suillus* Ackert and Payne, 1922. The worms were, on the average, slightly smaller than those from man, and the authors have pointed out a number of small characters in which they appeared to differ from *N. americanus*. Among these one of the most striking is the length of the spicules, which were little more than half the average length observed in the human form (0.325 to 0.469 mm.). Gordon, however, has made a comparative study of *Necator* from pigs and human beings in Amazonas, and concludes that there are no constant differences between them. He finds that there is great variation in all the characters relied upon by Ackert and Payne, while the ratio of the length of the spicules to the length of the worms is practically constant.*

* Pigs appear to be difficult to infect experimentally with *N. americanus*, and Ackert and Payne concluded from the results of their attempts that they could not be so infected. Since, however, "*N. suillus*" was found post mortem in five out of six pigs used by them, this conclusion, as Gordon has pointed out, rests entirely upon their ability to distinguish between *N. suillus* and *N. americanus*. In any case the infections were always light in pigs, and it seems probable that the pig is not well adapted as a host for *Necator*.

The genus **Globocephalus** Molin, 1861 (= *Characostomum* Railliet, 1902; *Crassisoma* Alessandrini, 1909; *Raillietostrongylus* Lane, 1923), consists of stoutish forms without leaf-crowns and usually without cutting-plates* at the anterior margin of the buccal capsule. The buccal capsule is deep and funnel-shaped or subglobular, and is supported anteriorly by an external chitinous ring. The mouth-opening is tilted dorsally. There may or may not be a pair of subventral teeth near the base of the buccal capsule. The dorsal gutter extends almost to the mouth-opening. The dorsal ray of the bursa is cleft only in its terminal portion, and its terminations are tridigitate. The spicules are slender and curved dorsally at their tips or bent into an S-shape. An elongate accessory piece is present. The vulva is in the posterior half of the body, relatively near the anus, and the uterine branches are opposed. The species occur in the small intestine of swine and monkeys.

It is uncertain how many species of *Globocephalus* occur in the pig. Five such species have been assigned to the genus, but it is possible that not more than three of them may be distinct. *G. longemucronatus* Molin, 1861, is very inadequately described, and according to some authors *G. samoensis* (Lane, 1922) is possibly identical with it. Yorke and Maplestone state that practically the only difference between the descriptions of the two forms is the apparent absence of the subventral teeth of the buccal capsule in Molin's species. There is, however, a considerable difference in the measurements of the total length of the worms. *G. connorfilii* Lane, 1922, is regarded by Cameron, who has examined the original specimens, as a synonym of *G. urosbulatus* (Alessandrini, 1909). We may, therefore, for the present assume that four species occur in swine. These may be distinguished as follows:

1. Length, male, 7 mm.; female, 8 mm. Known distribution, Italy.

G. longemucronatus Molin, 1861.

2. Length, male, 4.5 to 5.5 mm.; female, 5.25 to 5.6 mm. Subventral teeth of buccal capsule large, bicuspid. Length of spicules 0.38 to 0.41 mm. Length of tail in female 0.07 to 0.1 mm. Known distribution, Samoa and New Guinea.

G. samoensis (Lane, 1922).

3. Length, male, 4.4 to 5.5 mm.; female, 5 to 7.5 mm. Subventral teeth usually small, simple. Length of spicules 0.54 to 0.59 mm. Length of tail in female 0.18 to 0.23 mm. Known distribution, Europe, Africa, Samoa, New Guinea, North and South America.

G. urosbulatus (Alessandrini, 1909).

* Lane states that in *G. [Raillietostrongylus] samoensis* there is a pair of very rudimentary "semilunes" in this position. Cameron considers the appearance of these due to an optical illusion.

4. Length, male, about 5 mm.; female, 6 to 7 mm. Subventral teeth variable in size, triangular. Length of spicules about 0.7 mm. Length of tail in female 0.132 to 0.166 mm. Known distribution, Java.

G. amucronatus (Smit and Notosoediro, 1926) Smit and Ihle, 1928.

In **Bunostomum** Railliet, 1902, the anterior end is bent dorsally, and the mouth has a pair of ventral cutting-plates. The buccal capsule is large and funnel-shaped, and near its base are a large dorsal tooth, carrying the dorsal gutter, and one or two pairs of smaller subventral lancets. The dorsal lobe of the bursa is asymmetrical. The right externo-dorsal ray arises high up on the main dorsal stem, and is long and slender. The left externo-dorsal ray is much shorter, arising at about the level of the bifurcation of the dorsal ray. The terminations of the dorsal ray are tridigitate. The

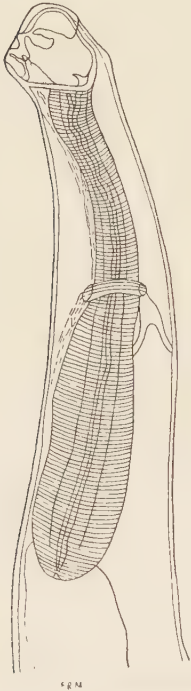


FIG. 118.—*Bunostomum trigonocephalum*: ANTERIOR END, LATERAL VIEW. (AFTER RANSOM.)

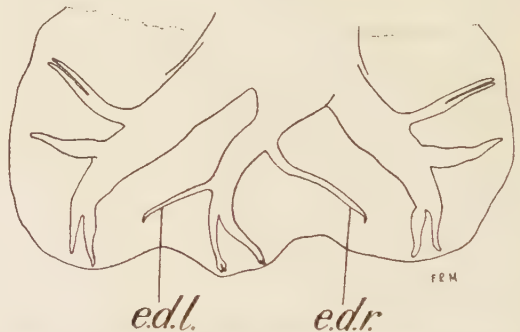


FIG. 119.—*Bunostomum trigonocephalum*: BURSA OF MALE, DORSAL VIEW. (AFTER RANSOM.)

e.d.l., left externo-dorsal ray; *e.d.r.*, right externo-dorsal ray.

spicules are slender, alate and unbarbed. The vulva is a little in front of the middle of the body, and the uterine branches are opposed.

Two species of this genus occur in the small intestine of ruminants. They may be distinguished as follows:

1. **B. trigonocephalum** (Rudolphi, 1808). Dorsal buccal tooth long; its dorsal border longer than the distance from its tip to the mouth-opening. Subventral lancets, one pair. Length, male, 12 to 17 mm.; female, 19 to 26 mm. Œsophagus 0.8 to 1.25 mm.

long. Spicules 0.6 to 0.64 mm. long, slightly twisted. Tail of female 0.25 to 0.275 mm. long. Hosts: Sheep, goat and ox. Distribution: Europe, N. America.

2. **B. phlebotomum** (Railliet, 1900). Dorsal buccal tooth short; its dorsal border shorter than the distance from its tip to the mouth-opening. Subventral lancets, two pairs. Length, male, 10 to 12 mm.; female, 16 to 19 mm. Œsophagus 1.25 to 1.5 mm. long. Spicules 3.5 to 4 mm. long. Tail of female 0.4 to 0.5 mm. long. Hosts: Ox, zebu and sheep. Distribution: Europe, America, Malay region.

In **Gaigeria** Railliet and Henry, 1910, the mouth-opening is oval and directed dorsally, and has a pair of cutting-plates ventrally. The buccal capsule is large and cup-shaped, and has at its base a pair of subventral lancets, in addition to a freely-projecting cone carrying the dorsal gutter. The bursa has a large dorsal lobe and two much smaller ventral lobes which are joined ventrally. The antero-lateral ray is short, blunt and widely separated from the other lateral rays. The externo-dorsal rays originate from the main trunk of the dorsal ray. The dorsal ray is cleft for about a quarter of its length, and its branches are stout and end in three very small digitations. The spicules have very slender, recurved terminations, without barbs. The vulva is just in front of the middle of the body.

The only known species, **G. pachyscelis** Railliet and Henry, 1910, occurs in the sheep and goat, and possibly in cattle, in India and Africa. The male measures up to 12 mm. in length, the female 16 to 17 mm. The Œsophagus is about 2 mm. long, and the spicules about 1.25 mm. The tail of the female is rather blunt and measures about 0.4 mm. in length.

In the genus **Uncinaria** Frölich, 1789, the mouth is directed slightly dorsally, and its opening is provided with a pair of ventral cutting-plates. The buccal capsule is large and funnel-shaped, and contains near its base a pair of subventral teeth. The dorsal cone does not project into the lumen of the capsule. The bursa has a short dorsal lobe and two large, separate lateral lobes. The antero-lateral ray diverges from the other lateral rays. The externo-dorsal rays originate at the base of the dorsal ray. The latter is cleft for almost half its length, and its terminations are tridigitate or occasionally bidigitate. The spicules are slender, with simple, filiform points. The tail of the female is bluntly rounded, but bears a slender terminal spike. The vulva is situated at about the posterior third of the body.

Uncinaria stenocephala (Railliet, 1884) occurs in the small intestine of the dog in Europe and North America, and has also been recorded from the pig in Canada. The male is 5 to 8.5 mm. long, the female

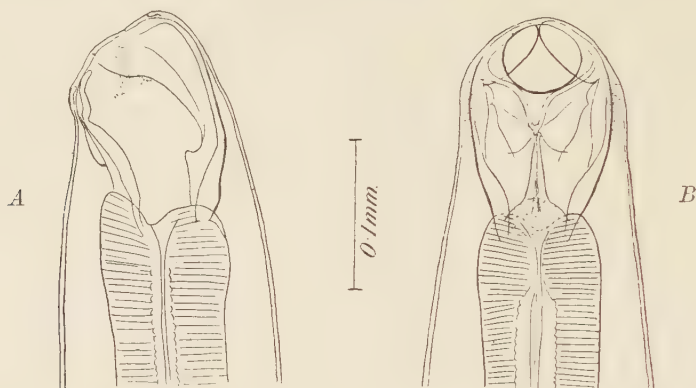


FIG. 120.—*Uncinaria stenocephala*: ANTERIOR END. (ORIGINAL.)

A, lateral view; B, dorsal view.

7 to 12 mm. The œsophagus measures 0.5 to 0.85 mm. in length, and the spicules 0.64 to 0.76 mm. The tail of the female is 0.15 to 0.29 mm. long.

The genus **Acheilostoma** Leiper, 1911, was erected for the reception of a form found in an African rodent, while Railliet has described another species, also from an African rodent. A species found in the intestine of a donkey in Brazil has also been referred to this genus, under the name of **Acheilostoma paranecator**, by Travassos and Horta, 1915. This is a worm measuring 8 to 10 mm. in length and 0.4 to 0.5 mm. in thickness in the male, 10 to 12 and 0.5 to 0.6 mm. respectively in the female. The anterior end is curved dorsally, and the mouth is more or less elliptical. The buccal capsule is small (0.1 mm. long), with two cutting-plates on its ventral edge, and two others in its posterior portion. On the surface of the dorsal wall there are three teeth (one median and two lateral). The median tooth contains the duct of the dorsal œsophageal gland. The œsophagus is club-shaped and 0.7 to 0.73 mm. long. The bursa of the male has a very small, bilobate dorsal lobe and two lateral lobes. The rays are said to include a pair of extra ventral rays (? prebursal papillæ). The dorsal ray is double, "arising in a common trunk with the posterolateral ray of the same side," and with bifurcate terminations. The tail of the female is 0.17 mm. long, and the vulva is in the middle region of the body. The uterine branches are divergent. The eggs are elliptical and measure 0.063 to 0.064 $\times$ 0.043 mm.

METASTRONGYLIDÆ.

The family *Metastrongylidæ** contains a number of forms parasitic in the respiratory and circulatory systems of mammals, and commonly referred to as "lungworms." These are generally rather slender and elongate worms, in which the buccal capsule is either greatly reduced or absent. The bursa of the male and its rays may be fairly well developed, but in some cases are much reduced or vestigial.

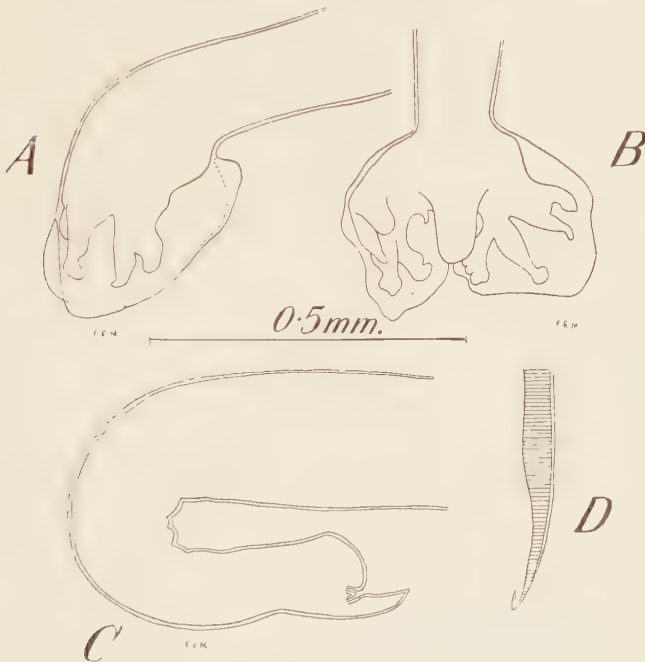


FIG. 121.—*Metastrongylus apri*. (AFTER GEDOELST.)

A, lateral view of bursa; B, ventral view of bursa; C, posterior end of female; D, tip of spicule. The scale refers to the figures above it.

In *Metastrongylus* Molin, 1861, the mouth is surrounded by six "lips," of which the two lateral are the largest. The bursa is relatively small, with a very small dorsal lobe and larger lateral lobes. Its greatest diameter is antero-posterior. Its wall is thickened in the posterior half, and all the rays are very stout except the dorsal and externo-dorsal, which

* The names in general use for certain genera of this family must, as Leiper (1926) has pointed out, be abandoned in favour of earlier names, in accordance with the law of priority. Thus *Synthetocaulus* becomes *Protostrongylus*, and *Hæmostrongylus* becomes *Angiostrongylus*. Since, however, the generic name *Metastrongylus* still stands, there appears to be no reason for following Leiper in changing the name of the family to *Protostrongylidæ*.

are much reduced. The antero-lateral ray is longer than the other rays and ends in a large, lobulate swelling. The spicules are long and end in simple hooks. The posterior end of the female is recurved ventrally. The vulva is immediately in front of the anus, and the uterine branches are parallel. The eggs contain fully-formed embryos when laid.

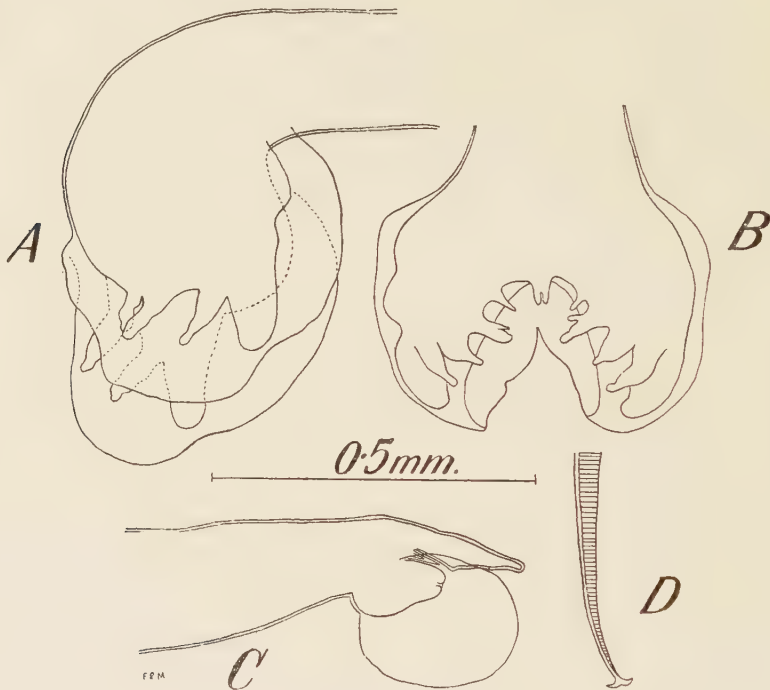


FIG. 122.—*Chærostrongylus pudendotectus*. (AFTER GEDOELST.)

A, lateral view of bursa; B, dorsal view of bursa; C, posterior end of female; D, tip of spicule. The scale refers to the figures above it.

Two species of this genus may be distinguished as follows:

1. **M. apri** (Gmelin, 1790) (= *elongatus* Dujardin, 1845) occurs in the lungs of the pig, and, accidentally, of man and ruminants. It is usually found in the bronchioles, more rarely in the bronchi. Length, male, 16 to 18.2 mm.; female, 12 to 58 mm. Œsophagus 0.5 to 0.63 mm. long, spicules (equal or subequal) 4 to 4.2 mm., tail of female 0.09 mm., vagina 2.3 mm. The eggs measure about 0.051×0.035 mm.
2. **M. salmi** Gedoelst, 1923, also occurs in the lungs of the pig. Length, male, 17 to 18 mm.; female 30 to 45 mm. Œsophagus 0.5 to 0.6 mm. long, spicules 2 to 2.1 mm., tail of female 0.095 mm., vagina 1.6 mm. The eggs measure about 0.054×0.037 mm.

Chærostrongylus Geddoelst, 1923, closely resembles the last genus, but differs from it in having a voluminous bursa in the male, the greatest diameter of which is at right angles to the long axis of the body, and whose wall is not thickened distally. The tip of the antero-lateral ray is not swollen. The spicules are long and end in double hooks. The posterior end of the female is straight, and there is a cuticular swelling covering the vulva and anus.

C. pudendotectus (Wostokow, 1905) (= *Metastrongylus brevivaginat*us Railliet and Henry, 1907) occurs in the bronchioles, and more rarely in the bronchi, of the pig. The male is 16 to 18 mm. long, and the female 19 to 37 mm. The œsophagus measures 0.48 to 0.56 mm. in length, the spicules (which may be equal or subequal) 1.2 to 1.4 mm., the tail of the female 0.175 mm., and the vagina 0.48 to 0.53 mm. The average size of the eggs is 0.06×0.04 mm.

In **Dictyocaulus** Railliet and Henry, 1907, there is a very shallow buccal capsule, with a chitinoid ring at its base. The bursa of the male is short, and the medio-lateral and postero-lateral rays are fused together, except at the tips. The externo-dorsal rays originate separately from the dorsal ray. The two branches of the latter have bidigitate or tridigitate terminations. The spicules are short, stout and simple, and show a reticulated structure. An accessory piece is present. The vulva is near the middle of the body, and the uterine branches are opposed. The eggs contain fully-formed embryos when laid, and may be without a chitinoid shell.

Three species of this genus occur in the bronchi of domesticated herbivora.

D. filaria (Rudolphi, 1809) occurs in the sheep, goat and deer in all parts of the world, and also in the camel. It has been recorded once by von Linstow from

cattle, but, even if this record be correct, is evidently very rare in these animals. The worms are whitish, the intestine showing by transparency as a dark line. The male measures 30 to 80 mm. in length, the female 50 to 100 mm. The spicules are 0.4 to 0.55 mm. long, and the eggs measure 0.112 to 0.135×0.052 to 0.067 mm. This species is a frequent cause of the disease known as verminous bronchitis,



FIG. 123.—*Dictyocaulus filaria* : POSTERIOR END OF MALE, LATERAL VIEW. (AFTER NEVEU-LEMAIRE.)

or "husk," in sheep, which often leads to a fatal form of pneumonia.

D. viviparus (Bloch, 1782) occurs in cattle and deer, and is of cosmopolitan distribution. It has occasionally, and perhaps erroneously, been recorded from the horse. The length of the male is about 40 mm., that of the female 60 to 80 mm. The spicules are 0.195 to 0.215 mm. in length, and the eggs measure about 0.085×0.035 mm. This species is often responsible for the occurrence of verminous bronchitis ("husk") in calves, not infrequently leading to death by suffocation.

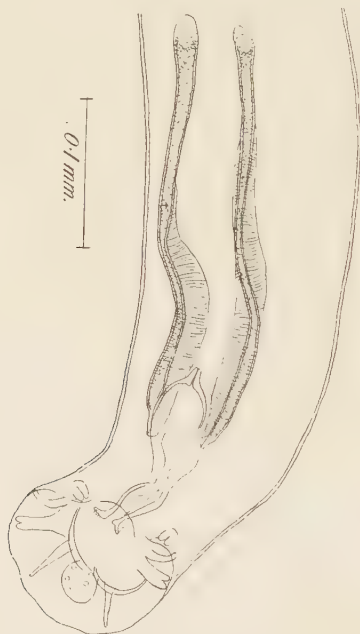


FIG. 124.—*Protostrongylus ocreatus* : POSTERIOR END OF MALE, VENTRAL VIEW. (ORIGINAL.)

D. arnfieldi (Cobbold, 1884) is a parasite of the horse and donkey, and, like the other species, often causes bronchitis, which may be fatal in severe cases. The male is 25 to 36 mm. long, the female 43 to 60 mm. The spicules are club-shaped and measure 0.2 to 0.25 mm. The eggs measure 0.08 to 0.1×0.05 to 0.06 mm.

In *Protostrongylus* Kamensky, 1905 (—*Synthetocaulus* Railliet and Henry, 1907), the body is extremely slender. The posterior end of the male is strengthened with a pair of chitinous arcs. The bursa is short, and the medio-lateral and postero-lateral rays are closely applied to each other. The dorsal ray consists of a very thick trunk with short

terminal digitations. The spicules are rather stout, striated or pectinated, and simple or bifid towards their tips. There are two accessory pieces, and a median chitinous structure possibly homologous with the "telamon" described for certain other Strongyle genera. The vulva is near the anus, and the uterine branches are parallel. The eggs are unsegmented when laid. The larva has an undulating terminal caudal process and a subterminal caudal spine.

The adult worms are reddish in colour when fresh, and occur in the finer bronchioles and in the connective tissue of the lungs of their hosts, sometimes producing pneumonia. Four species, occurring in sheep and other domestic animals, may be distinguished as follows:

P. rufescens (Leuckart, 1865) in sheep, goat and rabbit (Europe, Africa, North America). Length, male, 16 to 28 mm.; female, 25 to 35 mm. Spicules 0.24 to 0.265 mm. long, tubular, with broad membranous expansions or sheaths, and pectinate on ventral surface distally. Accessory pieces about 0.05 mm. long, partly fused anteriorly, and each with three or four strong teeth posteriorly. Eggs 0.075 to 0.12 × 0.045 to 0.082 mm.

P. ocreatus (Railliet and Henry, 1907) in sheep. Length, male, about 15 mm.; female, 24.5 mm. Spicules pectinate, 0.25 to 0.33 mm. long. Accessory pieces "top-boot-shaped," 0.04 to 0.075 mm. long, without teeth.

P. unciphorus (Railliet and Henry, 1907) in sheep and goat. Spicules 0.25 to 0.26 mm. long, pectinate, with rounded, hirsute tips. Accessory pieces hooked, 0.05 to 0.06 mm. long.

P. linearis (Marotel, 1913) in sheep (South of France). Spicules pectinate, unequal, the longer 0.32 to 0.36 mm., the shorter half as long. Accessory piece said to be single and gutter-shaped, 0.055 to 0.07 mm. long. This is a little-known species, and may prove to belong to a distinct genus.

The genus **Muellerius** Cameron, 1927, has been erected for the reception of a species, **M. capillaris** (Müller, 1889), formerly referred to the last genus. This is probably the commonest lungworm of the sheep, and occurs also in the goat, inhabiting the bronchioles and alveoli, and frequently causing bronchitis and broncho-pneumonia. The adult worms also wander into the connective tissue of the lungs, where they are enclosed in capsules or "worm nodules" and ultimately become calcified. The male worm measures 12 to 14 mm. in length. Its posterior end is spirally coiled, and instead of the usual bursal

rays is provided with a few pairs of small papillæ. According to Cameron there is no accessory piece, but a small "telamon" is present, consisting of two conical rods, 0.013 mm. long. The spicules are equal,

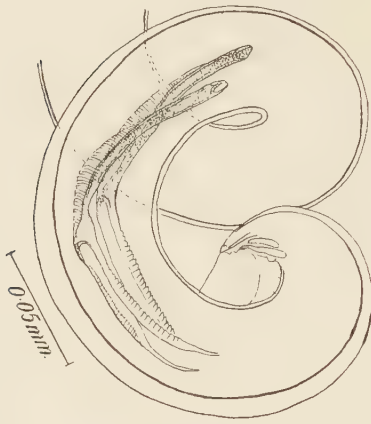


FIG. 125.—*Muellerius capillaris*:
POSTERIOR END OF MALE,
LATERAL VIEW. (ORIGINAL.)

measuring 0.14 to 0.18 mm. in length, and are bifurcated and sharply pointed distally, serrated on their ventral surfaces and provided with membranes or sheaths. The female is 19 to 23 mm. long. The vulva is close to the anus, and has a slight cuticular swelling on its posterior lip. The uterine branches are parallel. The eggs measure about 0.1 mm. in length, and their contents are unsegmented when laid. The larvæ resemble those of *Protostrongylus rufescens* in possessing an undulating caudal appendage.

The genus *Ælurostrongylus* Cameron, 1927, has also been erected for a species

formerly included in *Synthesetocaulus*—namely, *A. abstrusus* (Railliet, 1898), a parasite of the lungs of the cat. in which animal it causes a form of broncho-pneumonia. This worm closely resembles *Protostrongylus*, but the "telamon" and the cuticular bursal arcs of the male are absent. The bursa is fairly well developed. The dorsal ray is broadly Y-shaped, and the lateral rays are all close together and widely separated from the ventral rays. The spicules are equal, tubular and bluntly pointed, and provided with broad, transversely striated, membranous alæ or sheaths. They measure 0.075 to 0.13 mm. in length. There is a small accessory piece, 0.015 mm. long, with a flat base and anterior and posterior prolongations. The male worm measures about 4 to 5 mm. in length, the female 9 to 9.9 mm. The vulva is near the anus, the vagina relatively long, and the uterine branches parallel. The eggs measure 0.06 to 0.085 mm. $\times$ 0.055 to 0.08 mm.

The life-history of this species has recently been investigated by Cameron (1927, 1928), who finds that the adults live in the pulmonary blood-vessels, and the eggs are carried into the capillaries of the lungs, where they hatch. The larvæ penetrate through the tissues into the alveoli, pass up the trachea and are swallowed and passed out with the fæces. They must then be ingested by mice, in whose muscles and subcutaneous tissue they reach the infective, encysted form. The

mouse is therefore an intermediate host, and the cat becomes infected by preying upon it.

The members of the genus **Angiostrongylus** Kamensky, 1905 (=*Hæmostrongylus* Railliet and Henry, 1907) are relatively stout worms, occurring in the circulatory and respiratory systems of carnivores. The bursa is small but typically formed. The ventral rays are fused except at their tips. The antero-lateral rays are divergent from the remaining lateral rays, which are fused proximally. The stem of the dorsal ray is stout, and its terminal branches very short. The externo-dorsal rays originate separately from the dorsal ray and are short. The spicules are equal, relatively long and slender, and there is no accessory piece. The vulva is in the posterior half of the body. The female is oviparous or viviparous, and the larvæ have an undulating caudal process and, at the anterior extremity, a small ventral button.

Angiostrongylus vasorum (Baillet, 1866) occurs in the right side of the heart and in the pulmonary arteries of the dog. The male measures 14 to 18 mm. in length. Its posterior end is somewhat coiled. The spicules measure 0.36 to 0.4 mm. in length. The female is 18 to 25 mm. long, and the eggs measure 0.07 to 0.08 × 0.04 to 0.05 mm.

Oslerus osleri (Cobbold, 1879) Hall, 1921 (= *Strongylus canis bronchialis* Osler, 1877), is a very imperfectly-described and little-known form found in nodules below the mucosa of the trachea and bronchi of dogs, each nodule containing several worms. The male worm measures about 4 mm. in length, the female about 6 mm., according to Cobbold's description, or, according to Blumberg and Rabe, the male is 5 mm. and the female 9 to 15 mm. long. The male is said to possess unequal spicules, measuring respectively 0.048 and 0.056 mm. The vulva of the female is near the posterior end.

Cobbold considered that this worm was not a Strongyle, and referred it to "*Filaria*." Hall has suggested, chiefly on the ground of the position of the vulva, that it is related to *Gongylonema*. Travassos, on the other hand, who has referred certain species from monkeys to the genus *Oslerus*, places it among the Metastrongylidæ. The habitat and described effects of the worm (the latter recalling the "husk" of ruminants) certainly seem to suggest Metastrongyle affinities, while there appears to be nothing in the available descriptions, except the fact that a bursa has not been observed, to contradict this. The bursa, however, in some genera of Metastrongylidæ, is very insignificant.

The life-history of most of the lungworms is probably direct and without an intermediate host. This is known to be the case with *Dictyocaulus filaria*, which may be taken as typical. The eggs of this

worm hatch in the lungs of the host soon after their deposition, and the larvæ ascend the trachea and are swallowed and passed out of the body with the fæces, though they may occasionally be coughed out from the mouth. Within a few days in the open they moult twice, both old cuticles being retained for a time. Within about ten days, however, the first cuticle is shed, and the larvæ reach the infective stage. They are now highly resistant to extremes of temperature and to drying (the larvæ of *Protostrongylus rufescens* are said to be capable of withstanding drying for fourteen months under experimental conditions). When the grass is wet with dew or rain they climb up the blades, either descending again or remaining coiled up and quiescent if the moisture evaporates. If swallowed by a suitable host, they apparently migrate by way of the blood-stream to the lungs, where they reach maturity about six weeks after infection. So far as is known, the infective larvæ are not capable of skin-penetration.

TRICHOSTRONGYLIDÆ.

The members of the family **Trichostrongylidæ** are mainly small, slender forms in which the buccal capsule (present in the larvæ) becomes vestigial or disappears altogether in the adult. The bursa of the male

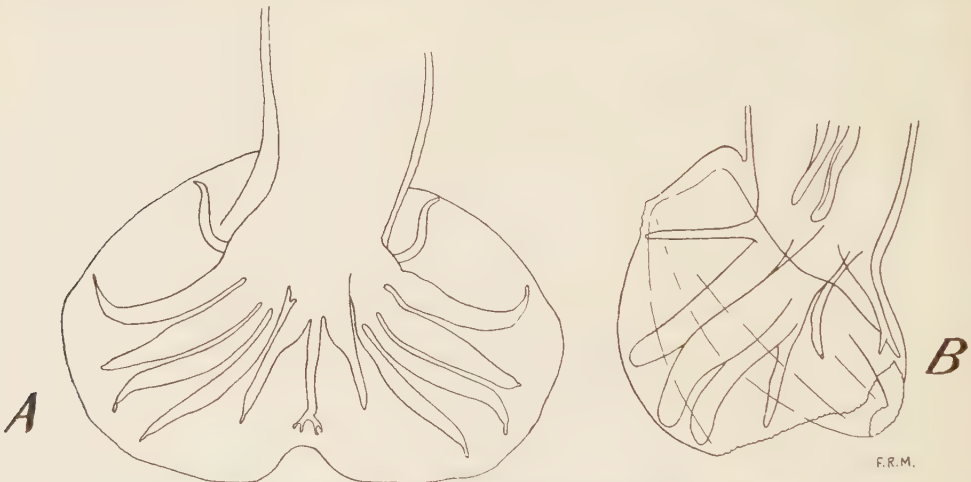


FIG 126.—BURSA OF (A), *Trichostrongylus extenuatus*, DORSAL VIEW (AFTER RANSOM); (B), *T. vitrinus*, LATERAL VIEW (AFTER LOOSS).

is well developed, with large lateral lobes but with a small or ill-defined dorsal lobe. The adult worms are parasitic in the alimentary canal of vertebrates.

In the subfamily **Trichostrongylinæ** the female genital tubes are paired, and the vulva is situated behind the middle of the body, but usually at some distance from the posterior end.

In *Trichostrongylus* Looss, 1905, the buccal cavity is ill defined. The ventral rays of the bursa are widely separated and of very different thicknesses, the ventro-ventral being thin and ventrally or anteriorly directed, while the latero-ventral is thick and more or less parallel with the lateral rays. The postero-lateral ray is thinner than, and divergent from, the remaining lateral rays, usually lying close to the externo-dorsal ray. The dorsal ray is cleft near its tip, each branch having two short terminal digitations. Small prebursal papillæ are present. The spicules are short and spoon- or spatula-shaped, often having a twisted appearance owing to the development of ridges or other projections on their surfaces. An elongate accessory piece is present. The vulva usually has prominent lips. The eggs are thin-shelled, and their contents are segmenting at the time of laying. The adults occur in herbivores, rodents, birds and man.

Seven species of *Trichostrongylus* occur in domesticated ruminants. They may be distinguished by means of the following key:

A. Spicules of male unequal in size. Postero-lateral ray of bursa as long as the other lateral rays.

- (a) Right spicule 0·085 to 0·095 mm. long, left spicule 0·11 to 0·12 mm., each giving off a slender, pointed, posteriorly directed process on its inner aspect near the middle. Accessory piece 0·05 to 0·06 mm. long. Male 3·4 to 4·4 mm., female 4·6 to 5·5 mm. long. Hosts: ox, sheep, goat. **T. extenuatus** (Railliet, 1898).
- (b) Right spicule 0·137 to 0·145 mm. long, left spicule 0·141 to 0·152 mm., each having on its ventral aspect a number of irregular transverse ridges and an angular projection towards the tip. Accessory piece 0·0864 mm. long. Male 4·5 to 6·6 mm., female 5·8 to 7·3 mm. long. Host: sheep (South Africa) **T. rugatus** Monnig, 1925.

B. Spicules of male equal in size. Postero-lateral ray of bursa usually considerably shorter and thinner than the other lateral rays.

- (i) Spicules more than 0·15 mm. long.

Spicules 0·16 to 0·17 mm. long, sharply pointed, without angular projections. Antero-lateral ray the thickest.

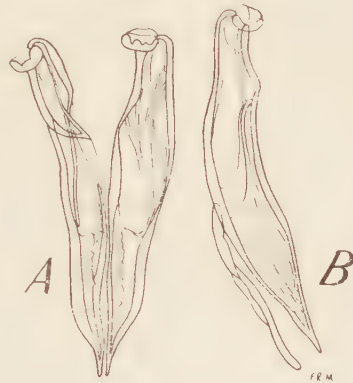


FIG. 127.—*Trichostrongylus vitrinus*:
SPICULES AND ACCESSORY PIECE.
(AFTER LOOSS.)

A, ventral view; B, lateral view.

Male 4 to 4·5 mm., female 5 to 6·5 mm. long. Hosts: sheep, goat, camel.....**T. vitrinus** Looss, 1905.

(ii) Spicules less than 0·15 mm. long.

(a) Spicules with an angular projection or "barb" on the ventral surface towards the tip. Postero-lateral ray much shorter than the other lateral rays.

1. Spicules relatively thick, 0·126 to 0·134 mm. long, with pronounced "barb" and in front of it a second angular projection. Latero-ventral ray much the thickest. Postero-lateral and externo-dorsal rays very short and close together. Tail of female 0·04 to 0·05 mm. long, rather blunt. Male 4·5 to 5·5 mm., female 4·5 to 6 mm. long. Hosts: sheep, camel....**T. probolurus** (Railliet, 1896).

2. Spicules relatively slender, 0·135 to 0·145 mm. long, with "barb" some distance from the tip, not very pronounced. Antero-lateral ray usually the thickest. Tail of female 0·055 to 0·07 mm. long, rather slender, sharply pointed. Male 4 to 5·5 mm., female 5 to 6 mm. long. Hosts: sheep, goat, camel.....**T. colubriformis** (Giles, 1892) (= *instabilis* Railliet, 1893).

3. Spicules 0·1 mm. long, with pronounced "barb" and with terminal portion slightly curved ventrally. Latero-ventral and antero-lateral rays of about equal thickness and thicker than the other rays. Postero-lateral ray slightly narrower than medio-lateral and curving away from it distally. Female unknown. Male 4·6 mm. long. Host: goat (South Africa).

T. falculatus Ransom, 1911.

(b) Spicules without angular projection, 0·13 to 0·145 mm. long, bent at an obtuse angle and much narrower in the distal portion. Latero-ventral ray the longest and thickest. Postero-lateral ray nearly as long as the other lateral rays. Male 4·3 to 4·9 mm., female 5·8 to 6·8 mm. long. Hosts: goat, sheep.....**T. capricola** Ransom, 1907.

Of the species tabulated above, several are known to occur also in various wild ruminants. Four of them (*T. colubriformis*, *T. vitrinus*, *T. probolurus* and *T. extenuatus*) are also occasional parasites of man.

Most of these forms inhabit the upper portion of the small intestine of their hosts, where they usually adhere to the mucosa. In ruminants, however, they are also found, either constantly or occasionally, in the abomasum (fourth stomach). Pure infections with a single species are rare in ruminants. When present in large numbers they may cause gastro-enteritis.

Trichostrongylus orientalis Jimbo, 1914, appears to be a common parasite of man in Japan, and to occur also in Korea, Formosa, and Armenia. The male measures 3.8 to 4.8 mm. in length, the female 4.9 to 6.7 mm. The latero-ventral ray is the thickest, the antero-lateral and medio-lateral successively thinner, and all curving ventrally. The spicules measure 0.119 to 0.133 mm. in length, and are nearly cylindrical in the

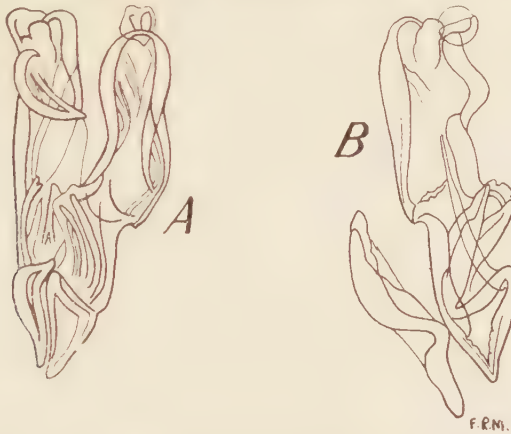


FIG. 128.—*Trichostrongylus probolurus*: SPICULES AND ACCESSORY PIECE.
(AFTER LOOSS.)

A, ventral view; B, lateral view.

distal third, with a blunt point and a barb close to it. The accessory piece is 0.065 to 0.084 mm. long. The ova measure 0.075 to 0.091 $\times$ 0.039 to 0.047 mm.

Trichostrongylus axei (Cobbold, 1879) occurs on the mucosa of the stomach of the horse and donkey, where, according to le Roux, it apparently sometimes causes superficial "ringworm like" lesions. The male is 3.8 to 6 mm. in length, the female 5 to 8 mm. The spicules are 0.11 to 0.15 mm. long. The eggs measure 0.1 to 0.112 $\times$ 0.063 mm. This species bears a very close resemblance to *T. extenuatus*, of which possibly it is really a variety.

Trichostrongylus tenuis (Mehlis, 1846) occurs in the caeca of the goose, duck, fowl, turkey, pheasant and partridge. It is very closely related to, but somewhat smaller than, *T. pergracilis* (Cobbold, 1873) (which is

regarded as being probably an important factor in the causation of "grouse disease"), and sometimes appears to produce similar pathological effects in young partridges. The male of *T. tenuis* measures 5 to 6.5 mm., the female 7.3 to 9 mm. in length. The spicules are about 0.13 to 0.15 mm. long.

The life-history of *Trichostrongylus*, for those species in which it has been studied, is simple and direct. The eggs are segmenting when laid and passed out of the host's body with the fæces. The development of the embryos usually takes place very rapidly in the open, and they hatch within eighteen to twenty-four hours. The first and second larval stages are passed, and the ensheathed, infective stage reached, during the next two to six days. The infective larvæ climb up low vegetation whenever there is sufficient moisture, and, if ingested by a suitable host, reach sexual maturity in from four to twenty-five days.

The genus **Cooperia** Ransom, 1907, contains four species parasitic in domestic ruminants. In this genus the cuticle surrounding the anterior



FIG. 129.—*Cooperia curticei*. (AFTER RANSOM.)
A, bursa, lateral view; B, spicules, ventral view.

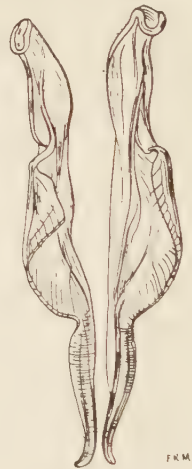


FIG. 130.—*Cooperia pectinata*: SPICULES, VENTRAL VIEW. (AFTER RANSOM.)

end is frequently dilated to form a vesicular swelling. The cuticle of the body is marked with fourteen to sixteen longitudinal lines or ridges. The bursa of the male has a small dorsal lobe. The latero-ventral ray is considerably thicker than the ventro-ventral, and is rather widely separated from it, but curves in the same direction towards its tip. The postero-lateral ray is slender. The externo-dorsal rays are long and originate high up on the dorsal stem. The dorsal ray is cleft for from one-third to one-half of its length, and its main branches may be parallel or curved

to form a lyre or horseshoe. From each main branch, usually near its origin, a short branch extends ventrally into a vesicular swelling on the inner surface of the bursa. The spicules are relatively short, broad and somewhat twisted. There is no accessory piece.

The following key to the species is taken, with slight modifications, from Ransom:

A. Spicules of male less than 0.2 mm. in length.

1. Branches of dorsal ray of bursa curved to form a lyre-shaped structure. Spicules 0.135 to 0.145 mm. long. Vulva of female a transverse slit. Male 4.6 to 5.4 mm., female 5.8 to 6.2 mm. long. Hosts: sheep and goat.

C. curticei (Railliet, 1893).

2. Branches of dorsal ray nearly straight, almost parallel. Spicules 0.12 to 0.15 mm. long. Vulva crescentic, elongated longitudinally. Male 4.7 to 5.9 mm., female 5.7 to 7.5 mm. long. Host: ox.

C. punctata (v. Linstow, 1907).

B. Spicules 0.24 to 0.3 mm. in length.

1. Main branches of dorsal ray rather widely divergent, forming a U-shaped arch with cleft tips. Spicules gradually tapering, with button-like terminations. Tail of female rather blunt, with a series of annular striations near the tip. Body much swollen in region of vulva. Combined length of muscular portions of ovejectors about 0.7 mm. Male 5.5 to 9 mm., female 6 to 8 mm. long. Hosts: ox and sheep.....**C. oncophora** (Railliet, 1898).

2. Main branches of dorsal ray rather close together, parallel, with undivided tips. Spicules with a prominently projecting, corrugated flange in the middle third. Tail of female sharply pointed, without annular striations. Combined length of muscular portions of ovejectors about 0.3 mm. Male about 7 mm., female 7.5 to 9 mm. long. Host: ox (North America and East Africa).

C. pectinata Ransom, 1907.

Hyoststrongylus rubidus (Hassall and Stiles, 1892) Hall, 1921, the only known representative of its genus, is a small, slender worm parasitic in the stomach of the pig. It is of a reddish colour when fresh, and the male measures 4 to 7 mm. in length, the female 5 to 9 mm. The cuticle is marked with forty to forty-five longitudinal striations, in addition to the usual transverse striations. The dorsal lobe of the bursa is small but distinct. The dorsal ray is bifurcate near the tip, and gives off a

pair of small lateral branches at about its posterior third. The ventral rays of each side diverge slightly, but the tip of the latero-ventral ray turns forward to end near that of the ventro-ventral. The postero-lateral ray is rather widely divergent from the other lateral rays. Pre-bursal papillæ are present. The spicules are 0.13 mm. long, broad and

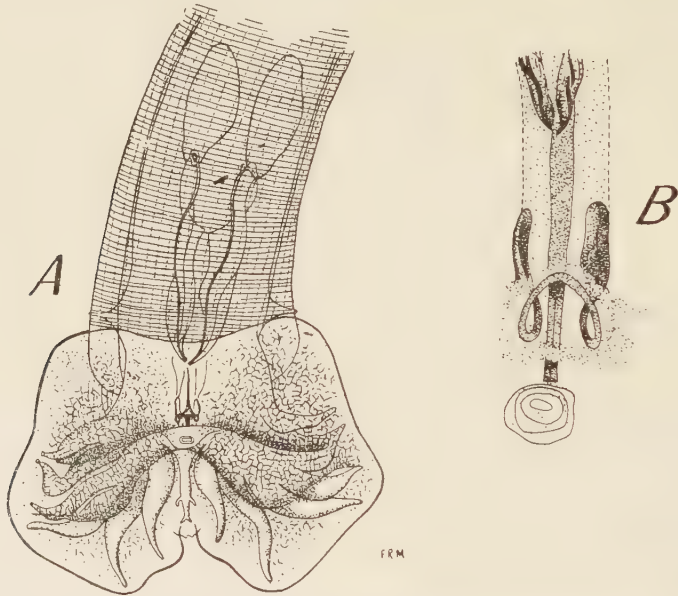


FIG. 131.—*Hyostrogylus rubidus*: A, BURSA, VENTRAL VIEW (FROM HALL, AFTER HASSALL AND STILES); B, "TELAMON" AND ASSOCIATED STRUCTURES (AFTER HALL).

membranous, and bifurcate distally. There is a narrow accessory piece, 0.06 mm. long, and also a characteristically shaped "telamon." The tail of the female is about 0.068 mm. long, and the vulva is situated at 1.3 to 1.7 mm. from the anus, with a small, crescentic cuticular fold just behind it. The eggs measure 0.045×0.036 mm., and their contents are segmenting at the time of laying.

In the genus *Ostertagia* Ransom, 1907, the cuticle of the body is marked throughout with a number (twenty-five to thirty) of longitudinal ridges. The cuticle of the anterior end may be slightly dilated. There is a small buccal capsule. The bursa of the male consists of two lateral lobes and a smaller dorsal lobe. The ventral rays are close together and parallel. The dorsal ray has two main branches, each of which gives off one or two accessory branches. Within the bursa, on the dorsal side (in some species at least) there is an "accessory bursal membrane" supported by two specially developed, slender, divergent rays. A pair of

prebursal papillæ is present. The spicules are relatively short, and are divided distally into two or three processes. An accessory piece may or may not be present. In some species the vulva of the female is covered by a cuticular flap developed from its anterior lip. The development of this flap varies considerably, however, even within the same species. The worms are parasitic in mammals, chiefly ruminants. A number of species occur in domestic ruminants, usually in the abomasum (fourth stomach), but sometimes also in the small intestine.

Ostertagia ostertagi (Stiles, 1892) occurs, either free or in nodules in the wall, in the abomasum of cattle. The male measures 6·5 to 7·5 mm.,

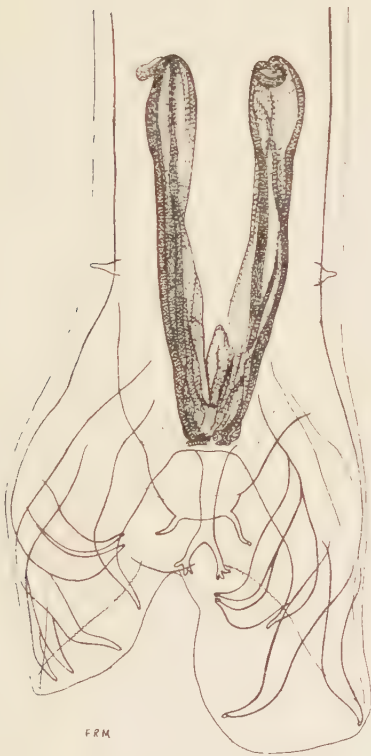


FIG. 132. — *Ostertagia ostertagi*: POSTERIOR END OF MALE, VENTRAL VIEW. (AFTER TRAVASSOS.)

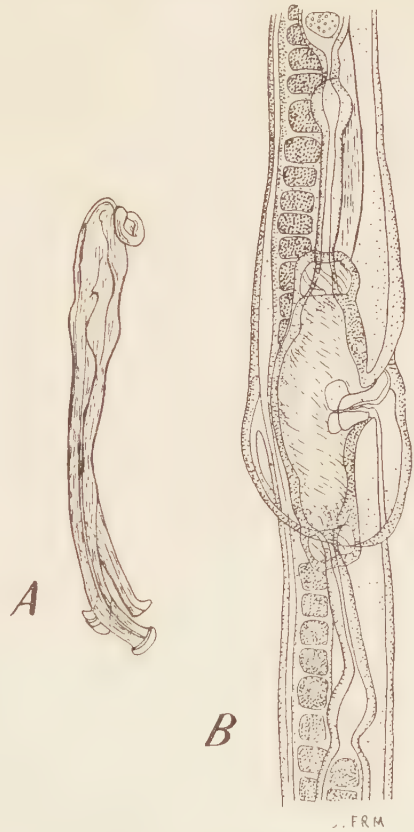


FIG. 133.—*Ostertagia ostertagi*. (AFTER RANSOM.)

A, spicules, lateral view; B, vulvar region of female.

the female 8·3 to 9·2 mm., in length. The main branches of the dorsal ray are bifid at the tip, and without secondary branches. The spicules are 0·22 to 0·23 mm. long, and each has two barbed processes on its

inner side in the distal half. The accessory piece is about 0.065 mm. long. The vulva is situated at 1.3 to 1.5 mm. from the posterior end, and is covered by a cuticular flap.

O. lyrata Sjöberg, 1926, which is recorded from the abomasum of cattle in Austria, appears to be, in most respects, very like *O. ostertagi*. This form measures 6.5 to 8.3 mm. in the male and about 7.5 mm. in the female. The dorsal ray has a long stem and very short terminal branches, which are bifurcate and carry a short accessory branch near the tip on the

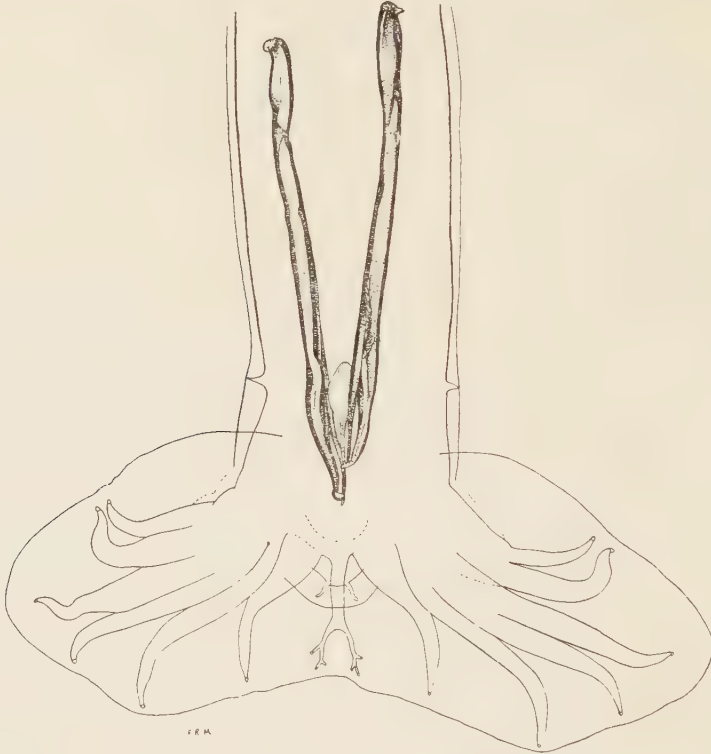


FIG. 134.—*Ostertagia circumcincta* : POSTERIOR END OF MALE, VENTRAL VIEW. (AFTER TRAVASSOS.)

outer side. The genital cone of the male has an appendage supported by a lyre-shaped chitinoid structure. The spicules are 0.196 to 0.225 mm. long, and are bifurcate distally, the outer branch being longer than the inner and curved inwards over its end. The accessory piece is about 0.063 mm. long. The vulva is about 1.3 mm. from the posterior end, and is without a cuticular flap. The tail of the female is about 0.167 mm. long, and ends in a knob-like enlargement.

O. circumcincta (Stadelmann, 1894) is a common parasite of sheep and goats. The male is 7.5 to 8.5 mm. long, the female 9.8 to 12.2 mm.

Each of the main branches of the dorsal ray has two short accessory branches, one on the inner side near the tip, the other on the outer side higher up. The spicules are bifurcate at the tips, with one process stout and knobbed, the other slender and pointed. They measure 0.28 to 0.32 mm. in length, while the accessory piece measures about 0.09 mm. The vulva, which is usually covered by a flap, is 1.9 to 2.3 mm. from the posterior end. A characteristic feature of the species, which enables it, with practice, to be recognized even under a low magnification, is the

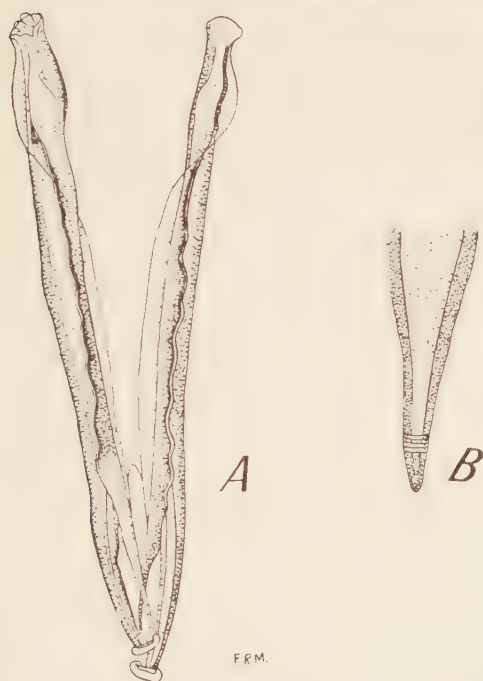


FIG. 135.—*Ostertagia circumcincta*. (AFTER RANSOM.)

A, spicules and accessory piece, ventral view;
B, posterior extremity of female.

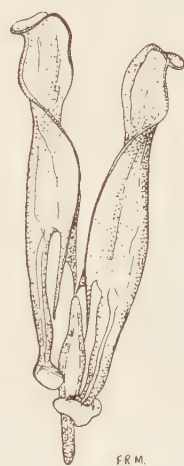


FIG. 136.—*Ostertagia trifurcata*: SPICULES AND ACCESSORY PIECE, VENTRAL VIEW. (AFTER RANSOM.)

presence, in the female, of a slightly raised band, composed of some three to five annular striations, near the tip of the tail.

O. trifurcata Ransom, 1907, also occurs in sheep and goats. The male measures 6.5 to 7 mm. in length. The dorsal ray is similar to that of *O. circumcincta*. The spicules are 0.18 mm. long, and have a stout outer process ending in a knob, and two slender, pointed, inner processes. The accessory piece is 0.07 to 0.09 mm. long.

O. marshalli Ransom, 1907, another parasite of sheep, and recently recorded from the goat, is a relatively large species, the male being 10 to

13 mm. long, the female 12 to 20 mm. The dorsal ray is very long and slender, and is bifurcated at about its posterior third, each branch being cleft at the tip and giving off a short accessory branch near the tip on the outer side. The spicules measure 0.25 to 0.28 mm., and are divided in the posterior quarter into three processes. There is no accessory piece. The vulva is situated at 2.5 to 5 mm. from the posterior end, and may or may not be overhung by a cuticular flap.

O. tricuspis Marotel, 1910, found in sheep in the Lyons district of France, appears to be very closely related to *O. marshalli*, but the bifurcated portion of the dorsal ray is relatively shorter, and the shape of the spicules, according to Marotel's figure, is different. The male is 10 to 12 mm. long, the female 14 to 16 mm. The spicules measure 0.2 to 0.25 mm. in length, and are stout and trifurcate at about their posterior fifth. The inner branch is sharply pointed and straight, the two outer branches also pointed but sinuous. An accessory piece is said to be absent, but there is a pentagonal, colourless structure (? telamon) apparently serving as a guide for the spicules. The vulva is "surrounded by a slight cuticular thickening" and situated at 3 to 3.3 mm. from the posterior end.

In **O. occidentalis** Ransom, 1907,* which also occurs in the sheep, and is a comparatively large form (male 12 to 16 mm.), the dorsal ray is similar to that of *O. marshalli*, but the spicules are longer (0.29 to 0.32 mm.). They are relatively stout, and are divided a little behind the middle into three processes, of which one is longer than the others and ends in a knob. There is an accessory piece measuring about 0.12 mm. in length.

O. bullosa Ransom and Hall, 1912, also found in sheep, is remarkable for the presence of a prominent ventral cuticular swelling in front of the bursa in the male. The length of the male is about 7.3 mm., that of the female 8.8 to 9.8 mm. The dorsal ray is similar to that of *O. marshalli*, but its main branches are very short. The spicules are 0.14 to 0.18 mm. long, and are tapering and pointed, but not forked. The accessory piece measures about 0.065 mm. The vulva, which sometimes has a very small cuticular flap, is at 1 to 1.3 mm. from the posterior end.

O. turkestanica Petrov and Schachovzeva, 1926, a form recently discovered in sheep and goats in Turkestan, is remarkable for its very long spicules (0.409 to 0.421 mm.), which are apparently divided into three processes at about the posterior sixth. The male is 9.8 to 10.64 mm. long, the female 12.5 to 13.5 mm. The dorsal ray is again much as in

* *O. trifida* Cuillé, Marotel and Panisset, 1911, found in sheep in France, appears to be very similar to this species, and is probably identical with it. As in *O. occidentalis*, the male only has been described.

O. marshalli, with relatively long main branches. The accessory piece measures about 0.07 mm. The female has a large vulvar flap.

O. mentulata Railliet and Henry, 1909, a form originally recorded from the camel, is 6.5 to 7.5 mm. long in the male and 8 to 10 mm. in the female. The spicules are remarkably long (up to 0.7 mm.) and conspicuously transversely striated. They terminate in a pair of pincer-like processes, about 0.09 mm. long and with hammer-shaped or button-like terminations.

A form very similar to that from the camel has been recorded by Marotel from sheep in France. Railliet and Henry, who examined Marotel's material, were of the opinion that it belonged to their species. The spicules, however, in the sheep material, were only 0.5 to 0.58 mm. long.

O. mentulata has also been recorded recently from the goat in Turkestan.

In ***Ornithostrongylus*** Travassos, 1914, the cuticle of the anterior end is inflated, and there is a slight buccal capsule. The ventral rays of the bursa are of equal thickness and close together. The postero-lateral

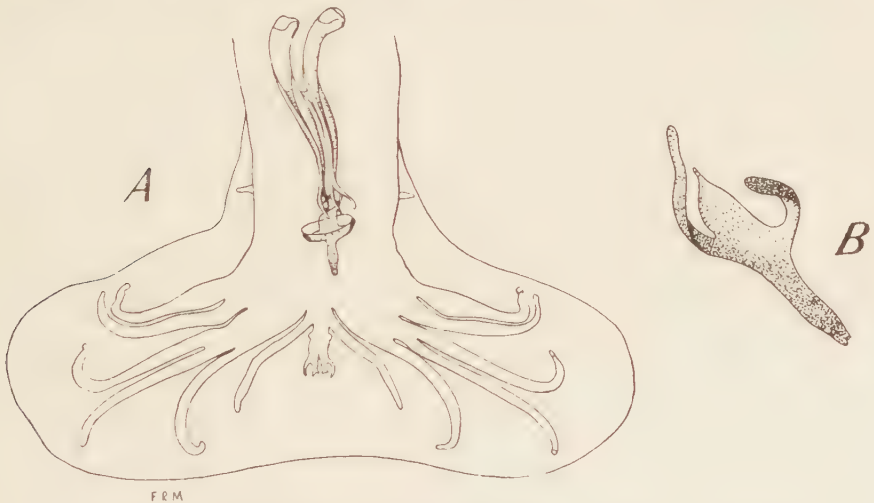


FIG. 137.—*Ornithostrongylus quadriradiatus*. (AFTER STEVENSON.)

A, bursa, ventral view; B, "telamon," ventral view.

ray is about as thick as the other lateral rays, but diverges from them. The main branches of the dorsal ray end in three or four digitations. Prebursal papillæ are present. The spicules are relatively short, and end in three points. A "telamon" (or an accessory piece?)* is present.

* In *O. quadriradiatus*, according to Stevenson's description and Irwin-Smith's figure, this structure is in the dorsal wall of the cloaca, and seems therefore to be an accessory piece. Hall, however, has stated that it is a telamon.

The vulva is in the posterior half of the body. The members of this genus occur in birds.

O. quadriradiatus (Stevenson, 1904) occurs in the intestine of the domestic pigeon in America. A form considered to be the same species



FIG. 138.—*Haemonchus contortus*: MALE. (AFTER NEVEU-LEMAIRE.)

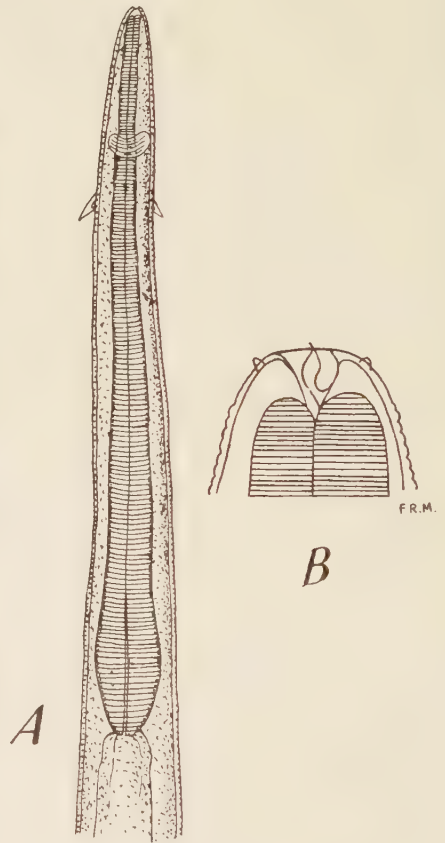


FIG. 139.—*Haemonchus contortus*: A, ESOPHAGEAL REGION, DORSAL VIEW (AFTER RANSOM); B, ANTERIOR END, LATERAL VIEW, MORE HIGHLY MAGNIFIED (AFTER YORKE AND MAPLESTONE).

has been described by Miss Irwin-Smith in Australia. Her measurements of it, however, differ considerably from those given by Stevenson.

The worms are reddish when fresh, and the female is often spirally coiled. The male measures (according to Stevenson) 9 to 12 mm. in length, the female 18 to 24 mm. The spicules measure 0.15 to 0.16 mm.,

and taper distally to end in three slender points. They are united by a membrane. The "telamon" is of a peculiar four-rayed form, with curved lateral processes embracing the spicules, and is 0.065 to 0.07 mm. long. The tail of the female is 0.14 mm. long, blunt, with but a fine terminal spike, and the vulva is situated at about 5 mm. from the posterior end. The eggs measure 0.07 to 0.075 $\times$ 0.038 to 0.04 mm.

The measurements given by Miss Irwin-Smith for Australian specimens are as follows:

Length, male, 6.2 to 6.8 mm.; female, 12.3 to 16.2 mm. Length of œsophagus, 0.352 to 0.51 mm. Length of spicules, 0.148 mm. Tail of female 0.14 to 0.156 mm. long. Vulva 2.25 to 3.33 mm. from posterior end. Eggs 0.067 $\times$ 0.039 mm.

In *Hæmonchus* Cobb, 1898, the body is reddish when fresh. A small buccal cavity is present, with a slender tooth or lancet originating from



FIG. 140.—*Hæmonchus contortus*: BURSA, DORSAL VIEW. (AFTER TRAVASSOS.)

the dorsal part of its base. There is a pair of very prominent, spine-like cervical papillæ. The bursa of the male has large lateral lobes and a small, very asymmetrical dorsal lobe arising from the left lateral lobe near its base. The ventral rays are separated towards their tips. The externo-dorsal rays are very long and slender. The main trunk of the dorsal ray originates with the left externo-dorsal ray in the left lateral lobe of the bursa, and is bifurcate distally. Prebursal papillæ are present. The spicules are relatively short and stout, and are provided with barbs at a little distance from their tips. An accessory piece is present. The

vulva is usually covered by a cuticular flap developed from its anterior lip, though the extent of development of this flap is subject to some variation even within the species. The contents of the eggs are segmenting at the time of laying.

This genus comprises the well-known "stomach-worms" of ruminants. Four species have been distinguished as occurring in domestic animals. The best-known form is *H. contortus* (Rudolphi, 1803), which occurs in the stomach (usually in the abomasum), and less commonly in the small intestine, of the ox, sheep, and goat, besides a number of wild ruminants. It is of world-wide distribution. This species has been recorded once

as a human parasite in the Argentine, doubtless as the result of an accidental infection.

The worms measure 10 to 20 mm. in length in the male, 18 to 30 mm. in the female. The maximum thickness is about 0.4 and 0.5 mm. respectively. The œsophagus is about 1.5 mm. long, and the cervical papillæ are situated at about 0.3 mm. from the anterior end. The stem of the dorsal ray of the bursa is little longer than its branches. The spicules measure 0.3 to 0.5 mm. in length, and end in small knobs or buttons. The left spicule has a barb on its outer surface at about 0.02 mm. from the tip, while the barb of the right spicule is at about 0.04 mm. from the tip. The accessory piece is fusiform, with thickened edges. The tail of the female is slender and sharply pointed, and measures 0.4 to 0.63 mm. in length. The vulva is situated at 3 to 4.5 mm. from the posterior end, and is usually covered by a large, tongue-shaped flap about 0.5 mm. long. The eggs measure 0.075 to 0.095 × 0.04 to 0.05 mm.

This parasite, when present in large numbers, is very injurious to its hosts. It frequently causes a fatal form of gastritis, accompanied by severe anæmia, in lambs. Its effects are probably due primarily to the habit of piercing the mucous membrane of the stomach and feeding upon blood.

Travassos has described two species of *Hæmonchus* from the abomasum of cattle in Brazil.

H. similis Travassos, 1914, is very like *H. contortus*, but apparently rather smaller. The male is 8.5 to 9 mm. long, the female 12 to 14 mm.

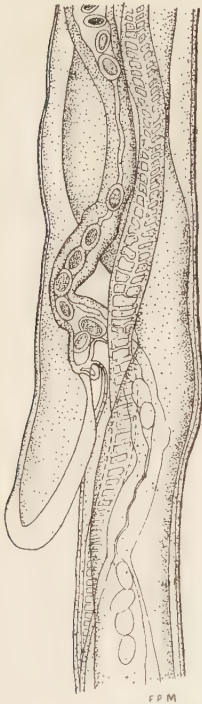


FIG. 141.—*Hæmonchus contortus*: VULVAR REGION OF FEMALE, LATERAL VIEW. (AFTER RANSOM.)

The cervical papillæ are at 0.319 to 0.34 mm. from the anterior end. The spicules are 0.319 to 0.333 mm. long, and have a button-like termination and a barb. In one spicule this barb is at 0.049 to 0.063 mm., in the other at 0.063 to 0.071 mm., from the tip. The accessory piece measures 0.156 mm. in length. The tail of the female is 0.2 to 0.24 mm. long. The vulva is situated on a conical elevation at 2.5 to 3 mm. from the posterior end, and the eggs measure 0.071 to 0.078 $\times$ 0.035 to 0.042 mm.

H. lunatus Travassos, 1914, is incompletely known, the description being based on a single, damaged male specimen. The spicules are quite different in character from those of *H. contortus*, being broader and not so gradually tapering. They are 0.234 mm. long, are twisted about their longitudinal axis, and end in a blunt tip. The accessory piece is broad and crescentic, with thickened edges, and measures 0.134 mm. in length.

Hæmonchus longistipes Railliet and Henry, 1909, occurs in the abomasum of the camel. It is a form measuring 20 to 21 mm. in length in the male, 26 to 29 mm. in the female. The dorsal ray has a stem twice as long as its branches, and the spicules are 0.625 mm. long.

The genus **Nematodirus** Ransom, 1907, contains a number of species of rather small, slender worms usually inhabiting the small intestine of herbivorous mammals. The anterior portion of the body is tapering and thread-like, but the cuticle at the anterior extremity is usually somewhat inflated. The cuticle of the body is marked with a varying number (usually at least eighteen) of longitudinal ridges. The anterior end of the œsophagus is eversible, and is armed with a small dorsal tooth and a pair of still smaller subventral teeth. The bursa of the male is composed of a pair of rather elongate lateral lobes, covered internally with rounded or oval cuticular bosses, and a pair of small dorsal lobes, more or less distinctly marked off from the former, and each supported by a separate dorsal ray. The ventral rays of each side are close together and parallel. The postero-lateral ray is close to the medio-lateral ray throughout the greater part of its length, only diverging from it slightly at the tip. The spicules are relatively long and slender, and are, in the majority of species, united together by a membrane except near their roots. There is no accessory piece. The tail of the female is short and abruptly truncate, except for a slender terminal spike. The vulva is typically situated at about the posterior third of the body. The eggs are relatively very large (generally, on the average, over 0.15 mm. long).

Several species of this genus occur in domestic ruminants. The males of the different species are not difficult to distinguish by the characters

of the bursa and spicules, but the females of several species are very much alike.

Nematodirus filicollis (Rudolphi, 1802) occurs in the ox, sheep, goat and certain wild ruminants in Europe and America. The male measures 10 to 15 mm. in length, the female 15 to 20 mm. The œsophagus is 0.4 to 0.6 mm. long. The bursa is large, with relatively slender rays and with large, elongate bosses. The dorsal lobes are not very distinct.

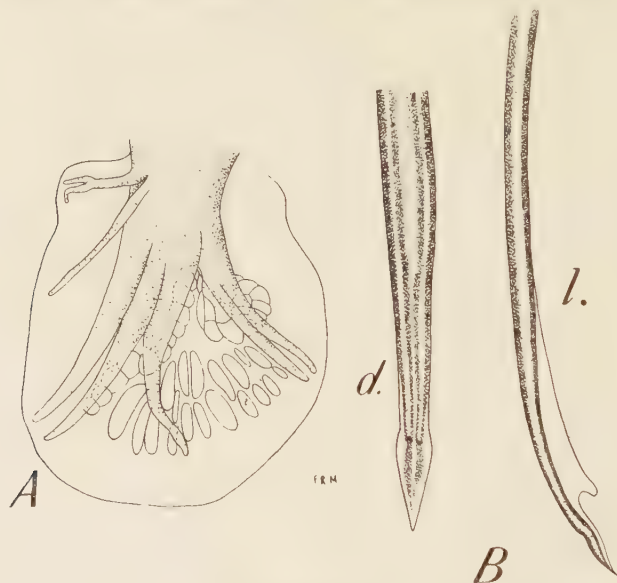


FIG. 142.—*Nematodirus filicollis*. (AFTER MAY.)

A, bursa, lateral view; B, dorsal (d.) and lateral (l.) views of tip of spicule.

The spicules are 0.68 to 0.95 mm. long, and end in a sharply pointed terminal piece. The tail of the female is 0.07 to 0.08 mm. long, and the eggs measure 0.13 to 0.2 × 0.07 to 0.09 mm.

N. spathiger (Railliet, 1896) occurs in the ox, sheep, goat, camel and certain wild ruminants and rodents, and is of almost world-wide distribution. The male measures 10 to 15 mm., the female 15 to 23 mm. The female is almost indistinguishable from that of *N. filicollis*. The male has a relatively small bursa, with distinct dorsal lobes and with few and small bosses. The spicules are 0.7 to 1.1 mm. long, and have a spoon-shaped terminal piece. The eggs measure 0.15 to 0.22 × 0.08 to 0.11 mm.

N. abnormalis May, 1920, is recorded from the sheep and goat in North America. The male is 11 to 17 mm. long, the female 18 to 25 mm. The latter is again very like that of *N. filicollis*. The male has a relatively small bursa, with stout rays and very distinct dorsal lobes. The bosses are numerous and small. The externo-dorsal ray runs close to the

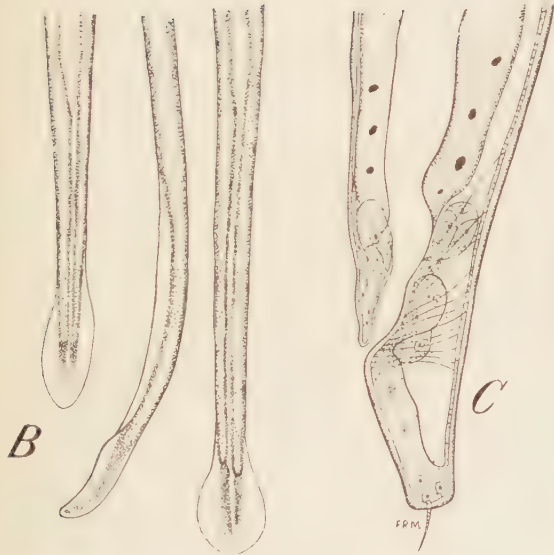


FIG. 143.—*Nematodirus spathiger*. (AFTER MAY.)

A, bursa, lateral view; B, a lateral and two dorsal views of the tips of spicules; C, posterior end of female, lateral view.

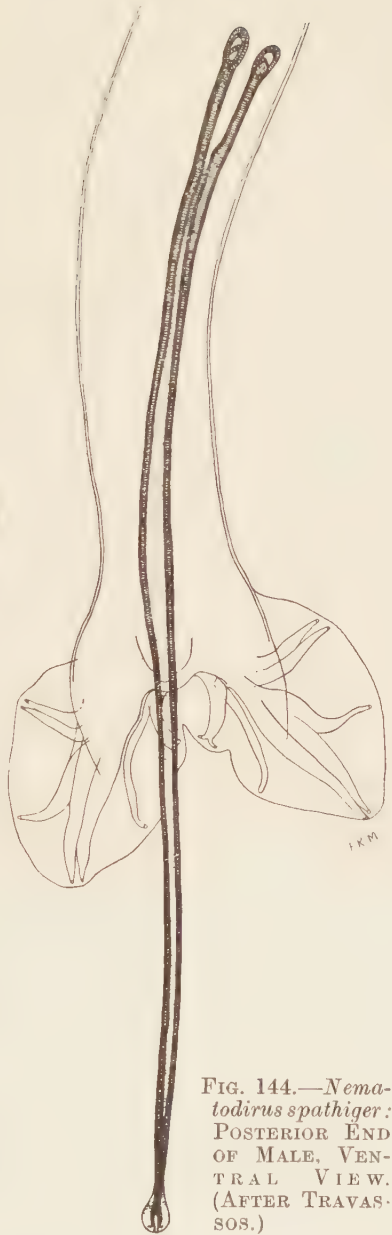


FIG. 144.—*Nematodirus spathiger*: POSTERIOR END OF MALE, VENTRAL VIEW. (AFTER TRAVASSOS.)

edge of the bursal membrane throughout its middle portion, but diverges from it towards its tip. The spicules are 0.9 to 1.25 mm. in length, and have a pointed terminal piece which is asymmetrical owing to the fact that the spicules are slightly unequal in length and twisted distally. The eggs measure 0.16 to 0.23×0.085 to 0.115 mm.

N. helvetianus May, 1920, found in the small intestine of the ox in Switzerland, closely resembles *N. abnormalis*, but the bursa of the male has less stout rays, and the tip of the externo-dorsal ray is nearer to the edge of the bursal membrane than its middle portion. The bosses are few and large. The spicules are 0.9 to 1.25 mm. long, and their terminal piece is symmetrical and sharply pointed, much like that of *N. filicollis*.

N. furcatus May, 1920, found in the sheep in North America, is a much smaller species, the male measuring only 6 to 6.4 mm. in length. The œsophagus is 0.3 to 0.45 mm. long. The bursa resembles that of *N. filicollis*, but has relatively longer and more slender rays and smaller bosses. The spicules are 0.5 to 0.8 mm. in length, and differ from those of other species in being separated throughout their distal third, and each ending in the form of an obliquely cut tube.

Two species have been recorded only from camels. These are *N. mauritanicus* Maupas and Seurat, 1912, and *N. dromedarii* May, 1920. They may be distinguished as follows:

N. mauritanicus : Male 13 to 15 mm.; female 21 to 24 mm. Œsophagus 0.575 to 0.61 mm. Bursa with dorsal lobes distinct from lateral lobes but united with each other. Spicules 4.5 to 5.5 mm. Tail of female 0.105 mm. long. Vulva at *posterior* third of body. Eggs 0.22 to 0.28×0.11 to 0.115 mm.

N. dromedarii : Male 10 to 15 mm.; female 20 to 29 mm. Œsophagus 0.5 to 0.6 mm. Bursa similar to that of *N. helvetianus*, with few bosses of granular appearance. Spicules 5 to 5.36 mm. Tail of female 0.145 to 0.15 mm. long. Vulva at *anterior* third of body. Eggs 0.23 to 0.26×0.1 to 0.12 mm.

In addition to the species mentioned, **N. leporis** Chandler, 1924, has been found in the duodenum of the domesticated rabbit in North America. This is a form measuring 8 to 13 mm. in the male, 16.5 to 20 mm. in the female. The dorsal lobes of the bursa are distinct, and the bosses small and numerous. The spicules measure 0.65 to 1.05 mm., are united for the greater part of their length and end in a membranous bulb. The vulva of the female is at about the posterior quarter of the body, and the eggs measure 0.16 to 0.18×0.08 to 0.09 mm.

The genus **Mecistocirrus** Railliet and Henry, 1912, is very closely related to *Nematodirus*. The longitudinal ridges on the cuticle are

numerous but inconspicuous. There is a pair of prominent, spine-like cervical papillæ. The mouth opens slightly towards the dorsal side, and contains a stout tooth or lancet. The bursa of the male has a single small dorsal lobe. The ventro-ventral ray is short, slender and widely divergent from the latero-ventral ray. The latero-ventral and antero-lateral rays are long, stout, close together and parallel. The rest of

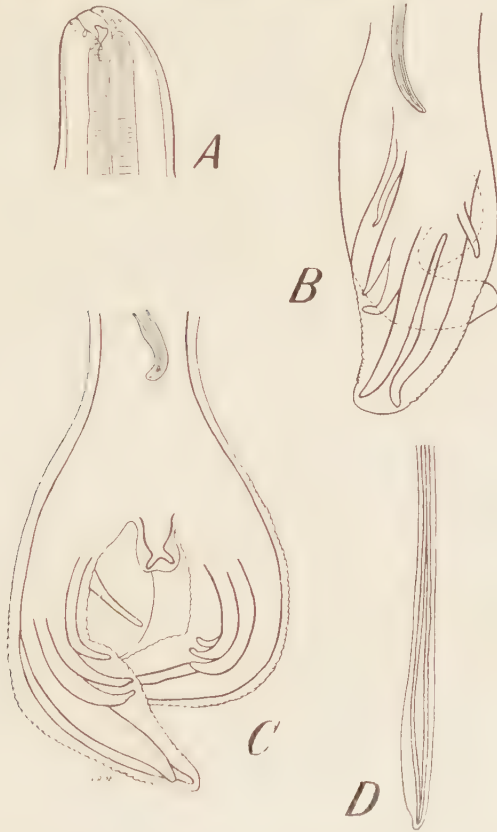


FIG. 145.—*Mecistocirrus digitatus*. (AFTER YORKE AND MAPLESTONE.)

A, anterior end, lateral view; B, bursa, lateral view; C, bursa, dorsal view;
D, tip of spicules.

the rays are shorter and more slender. The dorsal ray is short and bifurcate, and has three pairs of papillary terminations. There is a pair of prebursal papillæ. The spicules are very long and slender, united for almost the whole of their length, and with an asymmetrical membranous expansion at the tip. There is no accessory piece. In the female, the vulva is situated close to the anus and has prominent, chitinous lips, and the vagina is very long.

A single species, *M. digitatus* (v. Linstow, 1906) (synonyms, *fordii* (Daniels, 1908), *gibsoni* (Stephens, 1909), *tagumai* Morishita, 1922), occurs in the stomach, and less commonly in the small intestine, of the zebu, ox, buffalo, sheep and pig, and has also been recorded from man, in Eastern countries. This species appears to be very variable in size, the male measuring 16 to 31 mm. in length, the female 19 to 43 mm., according to different observers. The cuticle bears about thirty longitudinal striations. The œsophagus is about 1.6 to 1.8 mm. long. The spicules vary in length between 3.8 and 7 mm. The tail of the female is 0.14 to 0.2 mm. long, and the vulva is situated at 0.26 to 0.6 mm. from the posterior end of the body. The eggs measure 0.095 to 0.12 $\times$ 0.05 to 0.06 mm.

The subfamily *Heligmosominæ* contains a number of genera of Trichostrongylidæ characterized chiefly by the fact that the female possesses but a single genital tube, which runs forward from the posteriorly-placed vulva. This subfamily is unimportant from the medical and veterinary point of view, since almost all its species occur only in wild mammals, chiefly rodents. One genus, however, possibly belongs to it which is of interest here. This is *Ollulanus* Leuckart, 1865, whose only known species, *O. tricuspis* Leuckart, is a parasite of the stomach of the cat. This is a minute form, the male measuring only 0.7 to 0.8 mm. in length, and the female 0.8 to 1 mm., with a maximum width of 0.035 to 0.04 mm. The body is colourless and usually has the anterior end somewhat coiled. The cuticle of the anterior end is invaginated to form a very small, subspherical buccal cavity. The œsophagus is about 0.2 mm. long, and slightly swollen behind. There is a pair of large, posteriorly-directed cervical papillæ. The bursa of the male is without a distinct dorsal lobe or a mid-dorsal incision. The ventral rays are separate but nearly parallel. The antero-lateral ray is much thicker than, but parallel to, the other lateral rays. The externo-dorsal rays originate from the stem of the dorsal ray at about its middle. The dorsal ray is relatively stout and bifurcate distally. The spicules are rather broad and are bifurcate for the greater part of their length, one portion ending in a sharp point, the other rather bluntly. They measure 0.05 mm. in length. There is no accessory piece. The somewhat truncate tail of the female is 0.03 to 0.04 mm. long, and typically ends in three short points or "cusps," but may occasionally show more. The vulva is situated at about the posterior sixth of the body, and there is a single uterus and ovary. The worms are viviparous, the body of the mature female usually containing from one to three relatively very large larvæ.

The foregoing description is taken from the account recently given

by Cameron of the morphology of the adult worm. Cameron has also studied the life-history of the parasite, and has found that the account of it given by Leuckart was due to the confusion of the larvæ with those of quite a different worm (*Ælurostrongylus abstrusus*, *supra*, p. 176). Leuckart believed that mice acted as intermediate hosts for *Ollulanus*, which was transmitted to cats through preying upon them. Cameron, however, finds that the larvæ develop in the stomach of the cat up to the third stage, and has given reasons for believing that they may be transmitted to other cats in the vomit. If ingested by another cat, they develop directly, in the mucous membrane and in the lumen of the stomach, into fourth-stage larvæ and finally into adults.

AMIDOSTOMIDÆ.

The family **Amidostomidæ** contains certain peculiar genera of Strongyloidea which are in some respects intermediate between the Strongylidæ and the Trichostrongylidæ, but appear to be rather more closely related

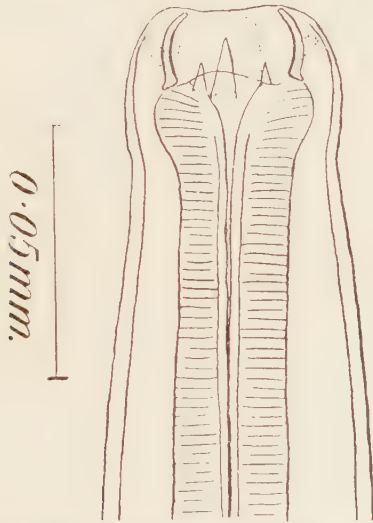


FIG. 146.—*Amidostomum nodulosum*: ANTERIOR END, DORSAL VIEW.
(ORIGINAL.)

to the latter family. The members of two of these genera occur in ducks and other aquatic birds, and are found usually under the cuticular lining of the gizzard, but sometimes also in or below the mucous membrane of the proventriculus or of the œsophagus. In these genera the buccal capsule, when present, is shallow but broad, and is without teeth, cutting-

plates or leaf-crowns at its margin. The œsophagus usually has three long chitinoid ridges or plates in its lining. The spicules of the males are relatively short, and are bifurcate or trifurcate distally. The vulva is in the posterior half of the body, and the two uterine branches are opposed. The body is usually reddish in the fresh condition.

In the genus **Amidostomum** Railliet and Henry, 1909, the buccal capsule is wide and thick-walled, and is provided with one or three

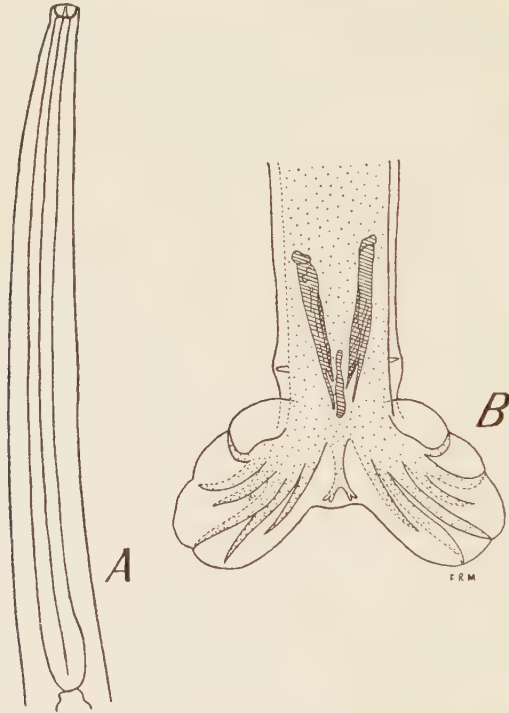


FIG. 147.—*Amidostomum nodulosum*: A, ANTERIOR END (AFTER BOULENGER); B, POSTERIOR END OF MALE, DORSAL VIEW (FROM YORKE AND MAPLESTONE, AFTER RAILLIET).

forwardly-directed teeth at its base. The bursa of the male has long lateral lobes and a short dorsal lobe. The two branches of the dorsal ray are short and have bidigitate terminations. Prebursal papillæ are present. The spicules are equal, and each is divided for the greater part of its length into two branches. An accessory piece is present. The tail of the female is long and finger-shaped.

Amidostomum nodulosum (Rudolphi, 1803) (= *Strongylus anseris* Zeder, 1800, in part) occurs in the domestic goose, as well as in many

species of wild geese and ducks. The male is 10 to 17 mm. long and 0.25 to 0.35 mm. thick, the female 12 to 24 mm. long and 0.3 to 0.4 mm. thick. The buccal capsule has three pointed teeth at its base. The spicules measure 0.3 to 0.35 mm. in length. The inner branch of each spicule has a spatulate tip. The accessory piece is slender and measures 0.095 mm. in length. The vulva is situated at about the posterior fifth of the body, and is sometimes covered by a cuticular flap. The eggs measure 0.085 to 0.11 × 0.05 to 0.082 mm., and contain embryos when laid.

In the genus *Epomidiostomum* Skrjabin, 1916, the head bears an armature consisting of backwardly-directed "epaulettes" or "festoons,"

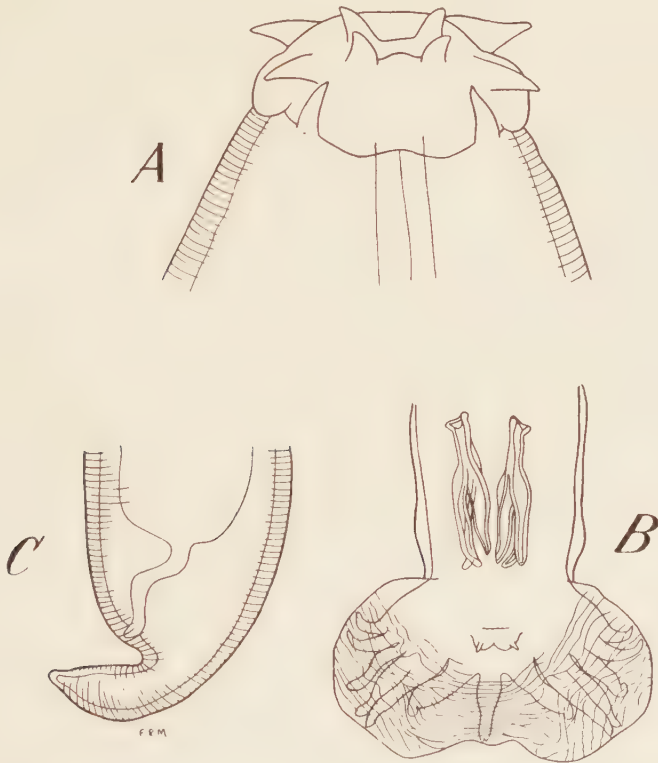


FIG. 148.—*Epomidiostomum skrjabini*. (AFTER PETROV.)

A, anterior end; B, posterior end of male, ventral view; C, posterior end of female, lateral view.

or a dorsal and a ventral pair of stout, backwardly-directed spines. The buccal cavity is much reduced or absent. The externo-dorsal rays of the bursa are short and thick. The terminations of the dorsal ray are

bidigitate. There is a pair of sessile papillæ on the lip of the cloaca. Prebursal papillæ are present. The spicules are short, equal, and divided distally into three branches. There is no accessory piece. The tail of the female narrows rapidly behind the anus and is bent ventrally. The contents of the eggs are segmenting at the time of laying.

Three species of this genus have been recorded as parasites of domestic ducks or geese, besides occurring in related wild birds. These may be briefly characterized as follows:

E. uncinatum (Lundahl, 1848) (= *anatinum* Skrjabin, 1916). Male 6.3 to 7.13 mm. long and 0.15 mm. thick. Female 10 to 11.5 mm. long and 0.25 mm. thick. Œsophagus 0.8 mm. long. Free edges of epaulette-like ornaments of head each with three tooth-like structures. Spicules 0.12 to 0.13 mm. long. Tail of female 0.14 to 0.17 mm. long, with a button-like termination. Vulva 2.2 mm. from posterior end. Eggs 0.074 to 0.08×0.048 to 0.05 mm. Host: duck.

E. orispinum (Molin, 1861). Male 10.8 mm. long and 0.21 mm. thick. Female 16.7 mm. long and 0.275 mm. thick. Head with two dorsal and two ventral backwardly-directed hook-like processes. Spicules 0.2 mm. long, with the dorsal branch longitudinally striated. Vulva at posterior fifth of body. Eggs 0.095×0.055 mm. Host: goose.

E. skrjabini Petrov, 1926. Male 9.5 to 11.5 mm. long and 0.21 to 0.24 mm. thick. Female 15 to 17 mm. long and 0.27 to 0.29 mm. thick. Head apparently bears twelve stout spines—four small, anteriorly directed, surrounding the mouth; four larger, outwardly directed; and four more behind these, anteriorly directed. Œsophagus 1.02 mm. long. Spicules 0.206 to 0.21 mm. Tail of female 0.156 to 0.175 mm. long. Vulva about 3.3 mm. from posterior end. Eggs 0.101 to 0.105×0.058 to 0.062 mm. Host: goose (Russia). It appears possible that this species may prove to be identical with *E. orispinum*.

THE ORDER FILARIOIDEA.

This order, as here understood (*i.e.*, as embracing not only the “superfamily” Filarioidea but also the “superfamily” Spiruroidea, or suborder Spirurata, of many authors) is a rather large assemblage of forms parasitic in vertebrates and chiefly characterized by the fact that the lips, when such structures are present, are paired and lateral in position. This condition has probably been derived from a primitively three-lipped condition. The six cephalic papillæ characteristic of almost all Nema-

todes are here again the rule, each of the lips (or each side of the head) carrying three of them (a lateral, a subdorsal and a subventral papilla). Occasionally, however, some of them are doubled. It is not infrequently stated that in some genera and species only the four submedian papillæ are present. The lateral pair may be very difficult to detect, and are often more pore-like than papilla-like, but it is probably safe to say that in every case, if carefully looked for in favourable and suitably prepared specimens, a pair of organs will be found to be present in this position.

The œsophagus, throughout the group, is without a specialized posterior "bulb," but is almost invariably composed of two more or less distinct portions—a narrower and shorter, purely muscular, anterior portion, and a wider and longer posterior portion, of a more granular and opaque appearance, and partially or wholly devoid of musculature. The œsophagus may or may not be preceded by a definite pharynx or vestibule.

The male worms usually possess more or less well-developed caudal alæ. Two spicules are usually present, and these are, in most cases, decidedly unequal in size and dissimilar in form. An accessory piece is often also present. The caudal end of the male is very frequently spirally coiled. The caudal papillæ are usually not very numerous, and may be sessile or may possess long peduncles which project into the alæ. The papillæ of the two sides are not infrequently asymmetrical in position, and sometimes in number. Asymmetry may also appear in other parts of the body in either sex, the cervical ala of the left side, for instance, being sometimes more highly developed than that of the right.

The females are usually very prolific, and either produce thick-shelled eggs containing embryos at the time of oviposition (*Spiruridæ*, *Gnathostomidæ*, etc.) or are viviparous or ovoviviparous (many *Filariidæ*).

Apart from the morphological characters above mentioned, the *Filarioidea* possess an important biological distinction from almost all other *Nematodes*, in the fact that, in all species whose development is known, an intermediate host is required for the larval stages. Among the *Filariidæ*, in all the species whose life-history has been elucidated, part of the development takes place in some kind of blood-sucking insect, which transmits the larvæ to a fresh host; while among the *Spiruridæ* the general rule appears to be for the larvæ to develop in some *Arthropod* or other small animal preyed upon by the final host.

FILARIIDÆ.

In the family *Filariidæ* the body is usually so much elongated in proportion to its thickness as to be described as thread-like. The mouth is usually without definite lips, or, when lip-like structures are present,

these do not carry the papillæ, which are situated behind or laterally to them on the surface of the head. As a rule there is no buccal capsule or pharynx. The male is generally considerably smaller than the female, and the spicules, as a rule, are unequal and dissimilar. The vulva of the female is situated not far from the anterior end of the body.

The adult worms occur in the connective tissue, blood-vessels, lymphatics or serous cavities of vertebrates, their presence not infrequently giving rise to the formation of nodules or tumours. The embryos are often surrounded at birth by a delicate membrane (probably representing the egg-shell) which adapts itself to the elongate form of the body, and is generally referred to as a "sheath." In some cases the embryos at birth are apparently without this "sheath," having hatched within the uterus of the parent, which is thus truly viviparous. The young worms, or "microfilariae," whether ensheathed or not, find their way into the blood-stream of the host or into the lymphatic system, whence they are able to be taken up, in the act of suction, by the appropriate intermediate host, or "vector," as it is frequently called. Further development does not occur until this has taken place.

It has been found that in some species there is a more or less definite adaptation between the habits of the microfilariae and those of their vector, in the "periodicity" of their occurrence in the peripheral circulation. Thus in *Wuchereria bancrofti*, whose vectors are mosquitoes which bite by night, the microfilariae are much more abundant in the peripheral blood by night than by day, and remain, during the waking hours of the host, in the more deeply situated organs and tissues. They are therefore said to have a "nocturnal periodicity." In *Loa loa*, on the other hand, whose vectors are flies which bite by day, the periodicity is diurnal. The microfilariae of these two forms were, in fact, named by Manson "*Filaria sanguinis hominis nocturna*" and "*F. sanguinis hominis diurna*." The "periodicity" is actually conditioned, however, by the sleeping habits of the definitive host, as is shown by the fact that it is capable of being reversed in *W. bancrofti* if the human host reverses his habits, sleeping by day and remaining active at night.

As regards the development of the larvæ in the intermediate host, the life-history of *W. bancrofti*, as established by Manson and many subsequent investigators, may serve as an example. In this species the embryos escape from their sheaths in the stomach of the mosquito within two hours or less of the infective feed. Within twenty-four hours they migrate from the stomach to the thoracic muscles, where they soon change considerably in form, becoming shorter and stouter and finally sausage-shaped, and also become quiescent. By the seventh day considerable changes have taken place in their internal anatomy, an

œsophagus and an intestine having become differentiated, and a body-cavity having appeared. During the following week a moult takes place, and the larvæ increase greatly in size, becoming much more elongate and recovering their activity. In a period of from twelve to twenty days in all they have completed their development, and begin to migrate from the thoracic muscles, chiefly in the direction of the head. Many of them penetrate into the labium, and when the mosquito feeds on human blood, they burst their way (often in pairs) through the thin membrane ("Dutton's membrane") at the end of this organ, and so arrive on the surface of the skin of the human host. This they penetrate by active effort, and not by entering the puncture made by the mosquito. Finally they arrive in some part of the lymphatic system, where they grow to sexual maturity.

The life-histories of other species which have been worked out conform in general to the same plan, differing only in details. *Loa loa* has been shown by A. and S. L. M. Connal (1922) to complete its larval development in *Chrysops* within ten to twelve days, during which time it increases tenfold in size. Dyce Sharp (1928) finds that in *Acanthocheilonema perstans* the larval growth is complete by the seventh day, and emergence from the vector (*Culicoides*) usually takes place on the eighth day.

The genus *Filaria* Müller, in the modern restricted sense, does not require consideration here, its genotype (and only species), *F. martis* Gmelin, being a parasite of certain wild mammals, chiefly of the weasel tribe. The name *Filaria*, however, continues to be largely used, in a loose sense, for Filariid worms whose status among the various modern genera has not yet been established. Many of these species, unfortunately, are very imperfectly known, and some of them are little more than names, with which the literature of helminthology, and more especially medical helminthology, is uselessly encumbered. Reference to some of these will be made below. They will, however, be placed after the forms whose generic status is more or less satisfactorily established, and it should be borne in mind that, though the name "*Filaria*" is used for them, it is not intended in the generic sense.

The genus **Parafilaria** Yorke and Maplestone, 1926, has been erected to contain a single species, **P. multipapillosa** (Condamine and Drouilly, 1878) (= *Filaria hæmorrhagica* Railliet, 1885). This is a parasite of the horse, donkey and mule, and occurs chiefly in Oriental countries or in animals of Eastern origin. It inhabits the subcutaneous and intermuscular connective tissue, and is the cause of a troublesome affection variously known as hæmorrhagic filariasis or parasitic dermatorrhagia. Slightly raised nodules (the "boutons hémorragiques" of French authors),

containing the adult worms, appear beneath the skin, and these break down and produce local hæmorrhages.

The adult male measures about 28 mm. in length and 0.26 to 0.28 mm. in thickness, the female 40 to 70 and 0.42 to 0.44 mm. respectively. The

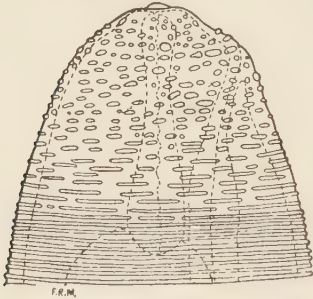


FIG. 149.—*Paraflaria multipapillosa*: ANTERIOR END OF FEMALE, LATERAL VIEW. (AFTER YORKE AND MAPLESTONE.)

cuticle of the anterior extremity is covered with numerous elliptical and circular papilliform elevations. There is a pair of small lip-like structures. The œsophagus is relatively very short. There are well-developed caudal alæ in the male, and a number of pedunculate preanal and postanal papillæ. The spicules are markedly unequal, measuring 0.68 to 0.75 and 0.13 to 0.14 mm. respectively. The tail of the female is bluntly rounded.

The anus is subterminal and apparently non-functional. The vulva is very close to the mouth. The female is oviparous, the eggs containing embryos when laid and measuring 0.025 to 0.058 $\times$ 0.024 to 0.033 mm. The embryos measure 0.22 to 0.23 $\times$ 0.009 to 0.011 mm. The life-history and intermediate host are unknown.

In the genus *Dirofilaria* Railliet and Henry, 1911, the mouth is without lip-like structures and the œsophagus is rather short and slender. The tail of the male is short and blunt. The posterior end of the body is spirally coiled, and provided with slight alæ, into which project pedunculate papillæ which are variable in number and usually asymmetrical. There is a group of voluminous preanal papillæ generally consisting of three to five pairs, and two pairs of ventral adanal papillæ. The postanal papillæ consist usually of one large pair and three smaller pairs close to the tip of the tail. The spicules are unequal and dissimilar, the longer terminating in a sharp point, the shorter stout and spatulate. The tail of the female is short and rounded. The vulva is situated at some distance from the anterior end, a little behind the œsophagus. The adults occur in the heart, blood-vessels and air-passages, or in the connective tissue, of various mammals. The female is viviparous, and the larvæ (without "sheaths") are found in the blood-stream of the host.

Dirofilaria immitis (Leidy, 1856) occurs in the dog and cat, as well as in various wild carnivores, and is widely distributed in the warmer countries of the globe. It inhabits chiefly the right ventricle of the heart and the pulmonary artery, where it may form dense masses, and is not infrequently a cause of death in dogs. It has also occasionally been found in the thoracic cavity, bronchi and other organs.

The male is 12 to 18 cm. in length, and usually has eleven caudal papillæ on each side, of which six are postanal. The spicules measure 0.318 and 0.2 mm. in length respectively. The female is 25 to 30 cm. long and 1 to 1.3 mm. in thickness. The vulva is situated at about 2.7 mm. from the anterior end. The microfilariae, measuring about 0.22 to 0.29 $\times$ 0.005 to 0.0065 mm., show a certain degree of nocturnal periodicity in the peripheral blood.

A number of mosquitoes are apparently capable of acting as vectors of this parasite, including *Anopheles maculipennis*, *A. bifurcatus*, *Myzorrhynchus pseudopictus*, *Myzomyia superpicta*, *Culex penicillaris*, *C. vexans*, *C. fatigans* and (rarely) *C. pipiens*.

Dirofilaria repens Railliet and Henry, 1911, is a smaller species found in the subcutaneous connective tissue of dogs in Europe and Asia. The male measures 48 to 70 mm. in length and 0.37 to 0.45 mm. in thickness, and has two to four preanal or adanal papillæ on one side and five or six on the other. The spicules measure 0.465 to 0.59 and 0.185 to 0.206 mm. respectively. The female is 100 to 170 mm. long and 0.46 to 0.65 mm. thick. The vulva is at 1.15 to 1.62 mm. from the anterior end. The microfilariae in the blood measure 0.207 to 0.36 $\times$ 0.005 to 0.008 mm.* The vectors are said to be *Stegomyia fasciata* and probably also *Anopheles maculipennis*.

Dirofilaria magalhãesi (Blanchard, 1895) is a form recorded once from the left ventricle of the heart of a child at Rio de Janeiro. The male measured 83 mm. in length and 0.28 to 0.4 mm. in thickness, and is described as having four pairs of preanal and four pairs of postanal papillæ, which were large and of mulberry-like appearance. The tail measured 0.11 mm. Only a single spicule (probably the shorter) is described. This measured 0.17 to 0.23 mm. The female was 155 mm. long and 0.6 to 0.8 mm. thick, with a tail measuring 0.13 mm. and the

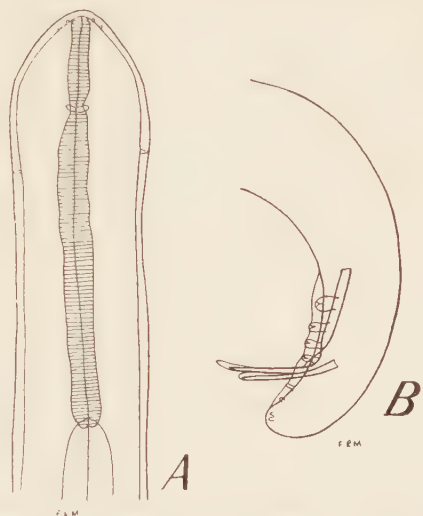


FIG. 150.—*Dirofilaria immitis*. (AFTER YORKE AND MAPLESTONE.)

A, anterior end, ventral view; B, posterior end of male, lateral view.

* The microfilariae from the blood of a dog in East Africa, named *Filaria ochmanni* by Fülleborn, are thought by Railliet, Henry and Langeron to belong to this species.

vulva situated at 2.5 mm. from the mouth. The measurements of the eggs are given as 0.038×0.011 mm.

In *Acanthocheilonema* Cobbold, 1870,* the body is generally very slender, and tapers markedly towards the posterior end. Near the tip of the tail in both sexes there is usually a pair of small lateral processes, sometimes giving the tail a trifid appearance. The head is blunt, and the four submedian papillæ may have double terminations. The caudal end of the male is spirally coiled, and usually without alæ. There are three or four pairs of preanal and two or three pairs of postanal papillæ. The spicules are very unequal and dissimilar, the left spicule being long, with a stout, tubular basal portion and a narrow, filamentous and sometimes alate distal portion; the right spicule short, usually much stouter and variable in shape. The tail of the female is moderately long. The females are viviparous, the microfilariae being without a "sheath." The adults occur in the serous membranes, connective tissue and vascular system of mammals, and the microfilariae in the blood.



FIG. 151.—*Acanthocheilonema perstans* : MICROFILARIA. (FROM CASTELLANI AND CHALMERS.)

A. perstans (Manson, 1891) is common in man in tropical Africa (where it also occurs in the chimpanzee and gorilla), and is recorded also from British Guiana and New Guinea. The adults are usually found in the connective tissue under the peritoneum and at the base of the mesentery. The male is about 45 mm. long and 0.06 to 0.08 mm. thick, and has four pairs of preanal and two pairs of postanal papillæ. The tail is about 0.12 mm. long, and has two triangular appendages at the tip. The female measures 70 to 80 mm. in length and 0.12 to 0.14 mm. in thickness. The tail is about 0.15 mm. long, and the vulva is situated at 0.6 to 1 mm. from the anterior extremity. The microfilariae have a bluntly rounded tail, and show no definite periodicity in the peripheral blood. Two types of

* Yorke and Maplestone (1926) consider this genus identical with *Dipetalonema* Diesing, 1861. This, however, depends upon the question of the identity of *D. caudispina* (Molin), the probable genotype of *Dipetalonema*. This imperfectly known species may be identical with *Acanthocheilonema gracile* (Rudolphi), since both are parasitic in South American monkeys. But in the absence of better evidence it seems wise to reserve judgment, and to retain the better-defined genus *Acanthocheilonema*.

microfilaria have been described as belonging to this species, one measuring 0.16 to 0.21 mm. in length and 0.005 to 0.006 mm. in thickness, the other smaller, measuring only 0.09 to 0.11 $\times$ 0.004 mm.

Dyce Sharp (1927, 1928) has recently found that a small midge, *Calicoides austeni*, acts as a vector of this species in the Cameroon, and has followed the complete development of the larvæ in it. This insect bites only in darkness. *C. grahami* is thought likely to be another vector. Partial development had previously been observed in certain mosquitoes—in *Taniorhynchus fuscopennatus* by Low, and in *Anopheles maculipennis* by Fülleborn—but it is not certain that the worm can be transmitted by these insects.

A. dracunculoides Cobbold, 1870, originally found in the Aardwolf of South Africa and in a hyæna, has been recorded from the peritoneal cavity of the dog in Tunis, and specimens taken from a dog in the Sudan have been identified by the writer as belonging to this species. The male measures 24 to 30 mm. in length, the female 32 to 60 mm. The tail has two conical subterminal processes, causing it to appear trifid. The vulva is situated at 1.3 to 1.85 mm. from the anterior end. The microfilariae measure 0.195 to 0.23 $\times$ 0.005 to 0.0055 mm., and have a very slender tail.

A. reconditum (Grassi, 1889), found in the connective tissue and perirenal fat of the dog in Italy, is a smaller form, measuring 12 mm. in length in the male, 26 to 30 mm. in the female, and about 0.1 to 0.16 mm. in thickness. The male has eleven pairs of caudal papillæ, of which one is preanal. The microfilariae measure 0.216 $\times$ 0.0043 mm.

A. grassii (Noè, 1907), found in the subcutaneous and intermuscular connective tissue and in the peritoneal cavity of the dog, is incompletely described. The female is 23 to 24 mm. long and 0.085 to 0.09 mm. thick. The microfilariae are said to possess sheaths, and, owing to their large size (0.567 $\times$ 0.012 mm.), not to circulate in the blood but to remain in the interstitial lymph of the connective tissue. According to Noè, the vector is a tick (*Rhipicephalus sanguineus*).

A. evansi (Lewis, 1882), which occurs in the arteries and in the mesentery of camels, may be briefly mentioned. It is a rather large form, measuring 75 to 90 mm. in the male and 170 to 215 mm. in the female.

In *Wuchereria* Silva Araujo, 1877, of Seurat, 1921, the body is slender and tapering anteriorly, but the head is slightly knob-like and wider than the neck. The mouth is simple and circular. There are two crowns of cephalic papillæ. The œsophagus is rather indistinctly divided into two portions. The tail of the male is digitiform, rather sharply curved ventrally and provided with alæ. The spicules are unequal, the longer tapering distally to form a long "lash" with delicate alæ, the shorter

gutter-like, of even width throughout, and coarsely marked distally. A small accessory piece is present. The tail of the female is rather long and bluntly rounded. The vulva is situated a little behind the middle of the œsophagus. The vagina is provided with a thick, pyriform ojector. The microfilariae are "sheathed."



FIG. 152.—*Wuchereria bancrofti*: ANTERIOR END OF FEMALE, LATERAL VIEW. (AFTER YORKE AND MAPLESTONE.)

The only certain species, *W. bancrofti* (Cobbold, 1877) is a widely distributed parasite of man in the warmer parts of the world. Cases have even been recorded in the South of Europe. The adult worms occur in the glands of the lymphatic system, and sometimes also in various internal organs and in abscesses. The male is 25 to 40 mm. long and about 0.1 mm. thick, and has about fifteen pairs of caudal papillæ. The tail measures about 0.13 mm., and the spicules 0.6 and 0.2 mm. respectively. The female varies in length from about 50 to 100 mm., and is 0.18 to 0.3 mm. thick. The tail is 0.17 to 0.28 mm. long, and the vulva is situated at 0.4 to 1.3 mm. from the anterior end.

The microfilariae measure about 0.26 to 0.3×0.008 mm. They normally display a somewhat marked nocturnal periodicity in the peripheral blood. The main features of the larval development have been described above (see p. 204). The vectors are mosquitoes of many species, among

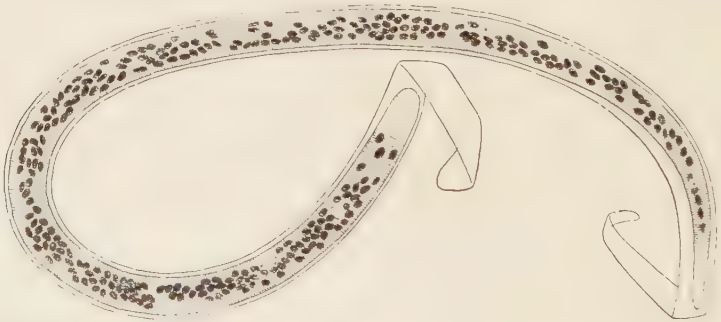


FIG. 153.—*Wuchereria bancrofti*: MICROFILARIA (FROM CASTELLANI AND CHALMERS.)

which the following have been incriminated: *Aedes pseudoscutellaris*, *A. togoi*, *A. variegatus*; *Anopheles albimanus*, *A. algeriensis*, *A. costalis*, *A. rossii*, *A. sinensis*; *Culex fatigans*, *C. pipiens*, *C. sitiens*; *Mansonioides africanus*, *M. uniformis*.

This species is believed by many authorities to be instrumental in the causation of several pathological conditions of the lymphatic system, and of elephantiasis. The case against it, however, is by no means conclusive, and it is, in any case, possible, as Dyce Sharp and others have suggested, that it may not be the sole causal agent, but that, in the regions where it occurs, *Onchocerca* may also play a part in these diseases.

The genus **Cordophilus** Monnig, 1926, has been erected for the reception of a species, **C. sagitta** (v. Linstow, 1907), which occurs chiefly in certain African antelopes, but is also recorded from the ox in Portuguese East Africa. It is found in the heart (either encysted among the muscles or free in the ventricles) and pericardium. In this species the body tapers anteriorly, and the head is slightly knobbed, as in *Wuchereria*. The œsophagus, in both sexes, is about 3 mm. long. The male is 57 to 85 mm. long and 0.7 to 0.73 mm. thick. The caudal end is spirally coiled and without alæ, and the tail is 0.115 mm. long. There are two pairs of preanal papillæ and an unpaired median papilla in front of the cloaca; four pairs of postanal papillæ close to the cloaca and a small pair near the tip of the tail. The spicules are unequal, the left measuring 0.5 to 0.55 mm., and having a membranous distal portion, and the right being 0.17 to 0.2 mm. long, more slender and slightly bent in the middle. The female measures 75 to 122 mm. in length and 0.85 to 1.2 mm. in thickness. The tail is about 0.2 mm. long, and the vulva is at 1.6 to 2.1 mm. from the anterior end. There is an S-shaped ovejector. The worm is viviparous, and the sheathless microfilarix measure 0.245 to 0.33×0.0075 mm.

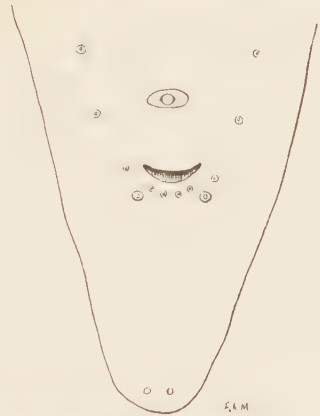


FIG. 154.—*Cordophilus sagitta*: POSTERIOR END OF MALE, VENTRAL VIEW. (AFTER MONNIG.)

The differences between this genus and the last are not very great, and it is possible, as has been suggested by Yorke and Maplestone, that the species should be referred to *Wuchereria*.

In the genus **Onchocerca** Diesing, 1841, both sexes are greatly elongate and thread-like. The cuticle is thick, and is remarkable for the presence, in addition to the usual transverse striations, of regular, spirally arranged thickenings, which are usually interrupted on the sides of the body by the lateral fields. In the male there is usually one such thickening for each striation; in the female the thickenings are at intervals of from two to

four striations. The mouth is without lip-like structures. The œsophagus is relatively short. The tail of the male is strongly curved, flattened ventrally and provided with narrow alæ. The caudal papillæ are variable in number and often asymmetrical, but almost always include a group of four pairs of adanal papillæ. The spicules are unequal, the longer being tubular in its basal portion and alate distally, with the alæ rolled inwards so as to form a tube; while the shorter is barbed at its extremity. The tail of the female is bluntly conical. The vulva is in the œsophageal region, and the worms are viviparous, the microfilariae being without "sheaths." The adults occur in the connective tissue and ligaments of mammals, sometimes in dense fibrous nodules in the interior of which several worms are inextricably coiled together.

Onchocerca volvulus (Leuckart, 1893) is a common parasite of man in tropical Africa. It lives probably at first in the lymphatic system,



FIG. 155. — *Onchocerca volvulus*: POSTERIOR END OF MALE, LATERO-VENTRAL VIEW (FROM STEPHENS AND YORKE, IN BYAM AND ARCHIBALD, AFTER RODENWALDT.)

ultimately coming to rest in the subcutaneous connective tissue, where it induces the formation of fibrous nodules. The male is 20 to 40 mm. in length and 0.13 to 0.2 mm. in thickness. The tail is 0.04 to 0.07 mm. long, and there are six or seven papillæ on each side. The spicules measure 0.13 to 0.23 mm. and 0.08 to 0.092 mm. respectively. The female may attain a length of 50 cm., or even possibly 70 cm., and a thickness of 0.3 to 0.36 mm. (complete specimens are almost impossible to obtain). The vulva is situated at 0.55 to 0.85 mm. from the anterior end. The eggs in the distal portions of the uterus measure 0.03 to 0.05 mm. in diameter, and have a pointed process at each pole ("like

an orange wrapped in tissue paper"). The microfilariae, measuring about 0.3×0.006 to 0.008 mm., are found in the skin of the host (occasionally in the blood or in hydrocœle fluid, urine, etc.).

Blacklock (1926) has shown that in West Africa *Simulium damnosum* is capable of acting as vector of this species.

O. cæcutiens Brumpt, 1919, is a closely similar form affecting man in Central America (Guatemala) and Mexico. It causes the formation of subcutaneous tumours, most commonly located on the head. The presence of these tumours on the head has been shown to be sometimes

the cause of affections of the eye, even leading to blindness in some cases. The male worm is 24 to 42 mm. long and 0.154 to 0.19 mm. thick. The caudal papillæ are asymmetrical, there being, according to Brumpt, three adanal papillæ on the right side and five papillæ on the left. The spicules measure 0.211 and 0.077 mm. The female attains a length of 50 cm. and a thickness of 0.3 mm. The vulva is at 0.8 mm. from the anterior end, and the eggs are without polar processes. The microfilariae measure 0.25×0.008 to 0.01 mm., and are not found in the peripheral blood.

Onchocerca reticulata Diesing, 1841 (*Spiroptera cincinnata* Ercolani, 1866), is a parasite of the horse, donkey and mule, occurring in the connective tissue, and especially in the flexor tendons of the foot, and in the suspensory ligament of the fetlock, in the foreleg. It produces fibrous nodules which are a frequent cause of lameness in these animals. The male measures 27 cm. or more in length and 0.15 mm. in thickness; the female 40 to 75 cm. or more, and 0.25 to 0.4 mm. respectively. The œsophagus is about 3.5 mm. long. The spicules of the male measure 0.2 to 0.26 and 0.1 to 0.12 mm., and there are six to ten caudal papillæ on each side. The vulva is at 0.4 to 0.58 mm. from the anterior end. The microfilariae, measuring 0.23 to 0.26 $\times$ 0.005 to 0.007 mm., occur in the lymphatics, connective tissue, synovial fluid, etc., and possibly also in the blood.

Another species, ***O. cervicalis*** Railliet and Henry, 1910, is said to be common in the cervical ligament of horses in France. The length of complete specimens is unknown. The male is 0.175 to 0.2 mm. thick, the female 0.4 mm. The œsophagus is 2.3 to 2.4 mm. long. The male has nine pairs of caudal papillæ, and the spicules measure 0.33 to 0.35 mm. and 0.1 to 0.12 mm. The vulva is at 0.375 to 0.41 mm. from the anterior end.

Several species of *Onchocerca* have been described from cattle. The best known of these is ***O. gibsoni*** Cleland and Johnston, 1910, which causes subcutaneous nodules in the ox and zebu in the Malay region and Australia. The male of this species is 30 to 53 mm. long and 0.14 to 0.19 mm. thick, and has six to nine caudal papillæ on each side. The spicules measure 0.14 to 0.22 mm. and 0.047 to 0.094 mm. The female measures up to 14 cm. or more in length and 0.35 to 0.6 mm.

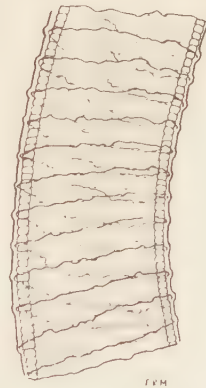


FIG. 156. — *Onchocerca cervicalis*: PORTION OF BODY OF FEMALE, SHOWING SPIRAL MARKINGS OF CUTICLE. (FROM NEUMANN, AFTER RAILLIET.)

in thickness. The vulva is at 0.46 to 1.18 mm. from the anterior end. The average length of the œsophagus, in both sexes, is about 0.75 mm. The microfilariae measure 0.22 to 0.35 $\times$ 0.003 to 0.004 mm.

Many unsuccessful attempts have been made to discover the intermediate host of this species among insects which bite cattle in Australia.

The other species found in cattle may be briefly characterized as follows:

O. indica Sweet, 1915. Hosts: zebu and buffalo in India and Ceylon. Forms nodules. Length, male, 33.8 to 93 mm.; female, up to 100 cm. Average length of œsophagus 1 to 1.23 mm. Male papillae generally eight to nine pairs. Spicules 0.207 to 0.274 mm., 0.08 to 0.094 mm., the shorter with shoe-shaped distal enlargement. Vulva 0.55 to 0.75 mm. from anterior end. Microfilariae 0.12 to 0.196 by about 0.002 mm.

O. gutturosa Neumann, 1910. Occurs in cervical ligament of ox in Northern Africa and Australia. Length, male, 28.3 to 33.8 mm.; female, 55 cm. or more. Length of œsophagus, male, 0.95 mm.; female, 1.15 mm. Male papillae six to seven pairs. Spicules 0.225 to 0.295 mm., 0.075 to 0.088 mm. Vulva 0.55 mm. from anterior end. Microfilariae 0.17 to 0.195 $\times$ 0.004 mm.

O. bovis Piettre, 1912. Occurs in connective tissue of ox in France, not forming nodules. Length, male, 40 to 55 mm.; female, 26 cm. or more. Length of œsophagus 0.75 to 0.85 mm. Male papillae seven pairs. Spicules 0.18 to 0.21 mm., 0.065 to 0.075 mm. Vulva 0.63 to 0.65 mm. from anterior end. Microfilariae 0.23 to 0.265 $\times$ 0.0055 mm.

O. armillata Railliet and Henry, 1909. Forms sinuous galleries in lining of aorta of ox, zebu and buffalo in Sumatra, the Malay States, Indo-China and India. Length, male, 50 to 90 mm.; female, 73 cm. Length of œsophagus 2.9 to 3.8 mm. Spicules 0.195 to 0.28 mm., 0.12 to 0.136 mm. Vulva 0.72 to 1.3 mm. from anterior end. Microfilariae 0.285 to 0.3 $\times$ 0.006 mm.

O. lienalis (Stiles, 1892) has been recorded from the capsule of the spleen, and the gastro-splenic ligament, of the ox in the United States and Australia.

Apart from their habitats, which seem to be to some extent distinctive, there appears to be very little difference between several of these species, and the careful comparison of further material from cattle might lead to the suppression of some of them.

Mention may be made here of **O. fasciata** Railliet and Henry, 1910, found in the subcutaneous tissue of camels. This species was based on

fragmentary material, and does not appear to have been fully described, although it has been recorded from Australia as well as India and Egypt.

Elæophora poeli (Vrijburg, 1897) Railliet and Henry, 1912 (= *Filaria blini* Carougeau and Marotel, 1903; *F. hamophila* v. Linstow, 1903) is a parasite of cattle and buffaloes, and is recorded from Indo-China, the Malay Peninsula, Sumatra, and the Philippines. The male is found in nodules in the wall of the aorta, while the female occurs with its anterior end buried in the nodules, and its posterior portion hanging free in the lumen of the vessel. The male is slender and filiform, and measures 45 to 70 mm. in length. Its cuticle is transversely striated at intervals of 0.014 to 0.018 mm. The female is 40 to 300 mm. long (on an average about 200 mm.). Its anterior (intra-nodular) portion is slender, measuring about 0.35 mm. in thickness, and bears cuticular striations at intervals of 0.02 to 0.022 mm. Its free posterior portion is much thicker (1.5 to 1.8 mm.), and its cuticle is smooth externally, though there are indications of internal striations.

The mouth is without lip-like structures. The œsophagus is very long (about 8 mm. in the male, 10 mm. in the female). The intestine is very narrow. The caudal end of the male is ventrally curved or coiled into a loose spiral, and without alæ. The tail is 0.1 to 0.11 mm. long. There are five pairs of small, sessile, caudal papillæ, of which two are preanal. The spicules are unequal, the longer measuring 0.192 to 0.25 mm. and having a blunt point, while the shorter measures 0.12 to 0.132 mm. and ends in a knob-like swelling 0.025 mm. long and 0.015 mm. wide. The tail of the female is 0.6 mm. long. The vulva is situated at a variable distance (0.65 to 1.35 mm.) from the anterior end. The vagina and common trunk of the uterus are long, the latter dividing dichotomously into four branches. The embryos measure 0.34 to 0.36×0.007 to 0.0075 mm., and are slightly swollen at the anterior end and tapering posteriorly.

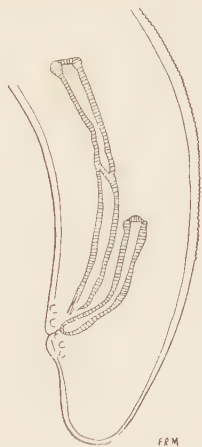


FIG. 157.—*Elæophora poeli*: POSTERIOR END OF MALE, LATERAL VIEW. (AFTER YORKE AND MAPLESTONE.)

The genus ***Setaria*** Viborg, 1795, contains a number of species parasitic in Ungulates, and inhabiting chiefly the peritoneal cavity. The mouth is surrounded by a raised, dorso-ventrally elongate, cuticular or chitinous ring which is notched laterally, and usually also dorsally and ventrally, so as to produce the impression of two or four forwardly-directed teeth.

The œsophagus consists of a short, narrow, anterior portion and a much longer and stouter posterior portion. The caudal end of the male is tapering and spirally twisted, and without alæ. There are four pairs of preanal papillæ and a median papilla just in front of the cloaca, three or four pairs of postanal papillæ and, usually, a pair of small lateral appendages near the tip of the tail. The spicules are very unequal and dissimilar, the left long, consisting of a tubular proximal portion and a membranous distal portion, the right short and of irregular shape. The posterior end of the female is also coiled into a loose spiral. The tail proper is conically tapering and curved dorsally, and bears a pair of lateral appendages near the tip, which is usually knobbed or spiny. The vulva is in the œsophageal region. The worms are ovoviviparous, the "sheathed" microfilariæ occurring in the blood of the host.

Setaria equina (Abildgaard, 1789) is a parasite of the horse, donkey, mule and zebra, and is of world-wide distribution. It occurs mainly in the peritoneal cavity, but occasionally in other situations (thoracic cavity,



FIG. 158.—*Setaria equina*: ANTERIOR END, LATERAL VIEW. (AFTER YORKE AND MAPLESTONE.)

lungs, testicles, even intestine). It has also been recorded from man and from the buffalo, and from the eye of the ox. The peribuccal ring, in this species, has four prominences, the two lateral being crescentic in outline, the dorsal and ventral truncate. The male is 48 to 80 mm. long and 0.4 to 0.6 mm. thick, the female 70 to 120 and 0.75 to 0.9 mm. respectively.

The anterior portion of the œsophagus is 0.53 to 1.1 mm. long, the posterior portion 7.4 to 13.3 mm. The tail of the male is 0.1 to 0.15 mm. in length, and the spicules measure respectively about 0.63 to 0.66 and 0.14 to 0.23 mm. The tail of the female is 0.475 to 0.6 mm. long, and ends in a knob. The vulva is situated at 0.41 to 0.69 mm. from the anterior end. The microfilariæ measure about 0.28×0.007 mm.

S. labiato-papillosa (Alessandrini, 1838) (= *Filaria cervina* Dujardin, 1845) occurs, chiefly in the peritoneal cavity, in the ox, African buffalo (*Bos caffer*), and various species of deer and antelopes. It is a widely distributed species. Filariids found in the eyes of horses have been referred to this species, but the determination is open to question. In this species, of the four processes of the peribuccal ring, the two lateral are crescentic in outline, the dorsal and ventral have their anterior borders notched. The male measures 40 to 60 mm., the female 60 to 120 mm., in length. The maximum thickness is 0.4 mm. in the male and 0.76 mm. in the female. The anterior portion of the œsophagus is 0.49 to 0.93 mm. long, and the entire œsophagus 6.1 to 9.5 mm. The tail of the male is

0.23 to 0.24 mm. long, and the spicules measure about 0.26 to 0.27 and 0.1 to 0.12 mm. respectively. The tail of the female is 0.43 to 0.65 mm. long and ends in a spiny knob. The lateral appendages are well developed. The vulva is at 0.46 to 0.83 mm. from the anterior end.

Setaria digitata (v. Linstow, 1906) is a form recorded from the peritoneal cavity of the zebu in Ceylon and Burma. A specimen found in the eye of a horse in Indo-China has been referred to this species, while the writer has also seen immature individuals from the eyes of horses in Ceylon which appeared more probably to be referable to it than to *S. equina* or *S. labiato-papillosa*. The lateral projections of the peribuccal ring, in *S. digitata*, are almost triangular and more prominent than in

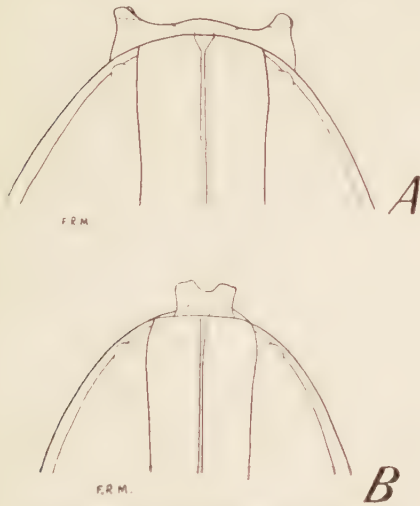


FIG. 159. — *Setaria labiato-papillosa* : ANTERIOR END. (AFTER BOULENGER.)

A, lateral view; B, dorsal view.

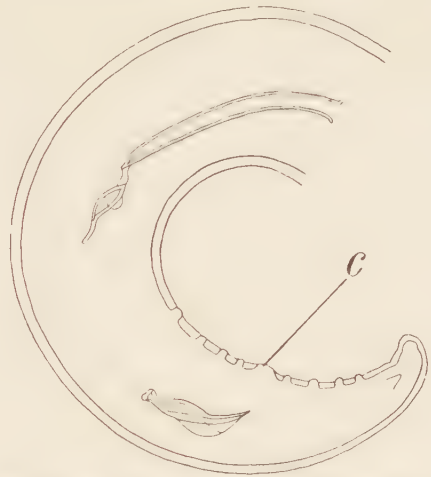


FIG. 160. — *Setaria labiato-papillosa* : POSTERIOR END OF MALE, LATERAL VIEW. (AFTER BOULENGER.)

c., position of cloacal aperture.

S. labiato-papillosa, while the dorsal and ventral projections are notched. The male is described by von Linstow as 42.5 mm. long and 0.55 mm. thick. The female, according to a recent redescription by Boulenger, is 62 to 78 mm. long and 0.5 to 0.68 mm. thick. The anterior portion of the œsophagus is 0.53 to 0.8 mm. long, the posterior portion 6.5 to 8 mm. The tail is 0.4 to 0.48 mm. in length, with large lateral appendages and a smooth terminal knob. The vulva is at 0.5 to 0.65 mm. from the anterior end.

Setaria marshalli Boulenger, 1921, is also recorded from cattle in Burma. The male is unknown. The female (of which a single specimen is described) is 90 mm. long and 0.6 mm. thick. The head is truncate.

The peribuccal ring has four very prominent processes, all bicuspid. The œsophagus is 9 mm. long. The tail measures 0.45 mm., and has a rounded end and two *bifurcated* appendages very close to the extremity. The vulva is about 0.6 mm. from the anterior end.

Setaria bernardi Railliet and Henry, 1911, is a form recorded from the peritoneal cavity of the pig in Indo-China. The mouth is surrounded by four processes. The œsophagus is described as measuring 0.75 to 0.8 mm. in length, but this probably refers to its anterior portion only. The length of the male worm is 100 to 110 mm., that of the female 200 to 210 mm. The tail of the male measures 0.192 mm. in length. The longer spicule has a basal portion 0.215 mm. long and a membranous distal portion of only 0.07 mm. The shorter spicule measures 0.14 mm. The tail of the female is 0.3 mm. long, and the rather prominent vulva is situated at 0.6 mm. from the anterior end.

In the genus **Loa** Stiles, 1905, the most characteristic feature is the presence, on the cuticle, of numerous small, irregularly distributed tubercles or "bosses." The mouth is without lip-like structures, and is placed at the apex of a truncate, conical process, which is narrower than the succeeding portion of the "head." Towards the base of this process are the usual lateral and submedian papillæ. The œsophagus is relatively short. The tail of the male is short and bluntly rounded, without alæ, and slightly curved ventrally. There are apparently nine pairs of caudal papillæ and two unpaired papillæ, the latter on the anterior and posterior lips of the cloaca. Of the former four pairs are large lateral papillæ with swollen peduncles, and form a group, three of which are preanal and one postanal. The remaining

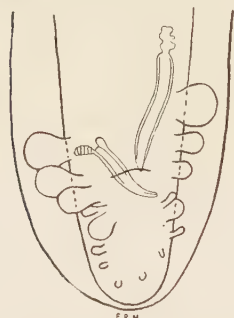


FIG. 161.—*Loa loa*: POSTERIOR END OF MALE, VENTRAL VIEW. (AFTER YORKE AND MAPLESTONE.)

papillæ are small and sessile. The spicules are unequal, but both short. The tail of the female is short and rounded. The vulva is postœsophageal. The common trunk of the uterus is long, and there are two uterine branches, both bending anteriorly at different levels.

The only certain species of this genus, **Loa loa** (Guyot, 1778), is a parasite of man in tropical Africa. It occurs chiefly in West and Central Africa, but also, less commonly, in East Africa. The adult worms inhabit principally the subcutaneous connective tissue, but are sometimes found in the serous membranes (*e.g.*, in the pericardium). Owing to their pronounced wandering habits they not infrequently appear in the conjunctiva of the eyes, while temporary swellings on the surface of the body

(especially on the wrist and forearm), known as "Calabar swellings," are generally thought to be the result of irritation set up by their migrations.

The male measures 25 to 35 mm. in length and 0.3 to 0.4 mm. in thickness, the female 45 to 63 and 0.4 to 0.5 mm. respectively. The tail of the male is about 0.08 mm. long. The spicules measure respectively 0.123 to 0.19 mm. and 0.088 to 0.115 mm. The longer spicule ends in two sharp points, the shorter has a rounded tip. The tail of the female is 0.17 to 0.265 mm. long, and the anus is somewhat prominent. The vulva is situated at 2 to 2.5 mm. from the anterior end. The worm is ovoviviparous, the "sheathed" embryos ("*Microfilaria diurna*" of Manson) appearing in the peripheral blood of the host during the day-time. They measure, when fresh, 0.25 to 0.3×0.0047 to 0.008 mm. In dried films their length is about 0.14 to 0.166 mm.

Manson, in 1895, first suggested that a biting fly of the genus *Chrysops* was probably the vector of this species. Leiper, in 1913, observed the development of the larvæ in *Chrysops dimidiata* and *C. silacea* under experimental conditions in Nigeria, while Kleine, in 1915, also found the larvæ in the same two species in the Cameroon. This observer noted that their development took place in the abdomen of the fly, the larvæ later migrating towards its head and emerging from its proboscis. More recently (1922) A. and S. Connal, working in Nigeria, have confirmed and extended these observations, and have given a very complete account of the development of the worm.

Some of the less known adult Filariidæ of man and domestic animals, whose systematic position remains uncertain, may now be briefly mentioned:

Filaria ozzardi Manson, 1897 (*F. demarquayi* Manson, 1897; *F. juncea* Railliet, 1908). Recorded from the mesentery and subperitoneal connective tissue of man in the West Indies, British Guiana and New Guinea. Female 65 to 80 mm. long, the tail measuring 0.23 to 0.25 mm. and having a pair of fleshy papillæ near the tip. Vulva 0.71 to 0.76 mm. from the anterior end. Microfilarix without "sheaths," measuring 0.2×0.005 mm. and showing no periodicity.

Filaria taniguchii Penel, 1905. Recorded from a lymphatic gland in a Japanese. Male unknown. Female 68 mm. long. Tail 0.23 mm. Vulva 1.3 mm. from anterior end. Microfilarix nocturnal, measuring 0.29×0.007 mm.

Filaria [Loa] extraocularis (Skrjabin, 1917). Immature female, 143 mm. long, found in a fibrous tumour of the eye of a Caucasian girl. Œsophagus 0.935 mm. long. Tail 0.1 mm. Vulva 2.04 mm. from anterior end. Though the worm is referred by Skrjabin to

Loa, the absence of cuticular bosses appears to exclude it from that genus.

Filaria conjunctivæ Addario, 1885 (= ? *F. inermis* Grassi, 1887; ? *F. apapillocephala* Condorelli-Francaviglia, 1892). In Addario's case a worm 95 mm. long was found in a growth removed from the conjunctiva of a woman in Sicily. Female worms found in the conjunctiva of man in Southern Europe and in India on other occasions have been referred to Addario's species, and are also considered by some authorities to be identical with forms found in the eyes of horses and donkeys. The status of all these forms, however, is rather uncertain.

Filaria capræ v. Linstow, 1883. A single female, in fragments and lacking its anterior portion, from the muscles of the tongue of a goat, apparently in Turkestan. The description merely states that the thickness of the worm was 0.36 mm.

Filaria cordicola v. Linstow, 1905. Recorded from the heart of the donkey and the peritoneal cavity of the horse in East Africa. Head said to be "without papillæ, lips, teeth or bristles." Male 65 mm. long, without caudal papillæ. Left spicule 0.23 mm. long, right 0.13 mm. Female (immature) 82 mm. long. Vulva divides the body in the proportion of 7:403.

Filaria spirovoluta Smit and Ihle, 1925. Recorded from the connective tissue below the pectoral muscles of the horse in Java, spirally coiled but not forming nodules. Male unknown. Female 95 to 132 mm. long and 0.272 mm. thick. Tail 0.32 mm. long, finger-shaped and ending in five conical processes. A granular mass below cuticle of head. Œsophagus very short and narrow, intestine much wider. Vulva postœsophageal, 0.88 to 1.13 mm. from anterior end. Viviparous. Embryos 0.16 to 0.19 × 0.0033 mm., found in blood of host. This worm may possibly belong to the genus *Acanthocheilonema*.

Agamofilaria Stiles, 1907. This is not a generic name, but a term suggested by Stiles for immature Filariidæ whose generic status is unknown. Under this heading may be mentioned the following doubtful species recorded from man:

A. oculi (v. Siebold, 1839) Stiles, 1907, in the eye.

A. palpebralis (Pace, 1867), in the eyelid.

A. georgiana Stiles, 1907, in the leg.

A. eiseni Ward, 1918, in the eye (doubtfully a worm).

Microfilaria Cobbold, 1880. This is not a generic name, but a collective name for the embryonic or larval stages of Filariidæ occurring

in the blood of the definitive host or in the body-cavity and tissues of the insect vectors. In addition to those mentioned already, the following forms, known only in this stage, are recorded from man:

M. powelli Penel, 1905.

M. philippinensis Ashburn and Craig, 1906.

M. romanorum Verdun, 1907.

M. nuda Rodenwaldt, 1914 (possibly = *Onchocerca volvulus*).

M. tucumana (Biglieri and Araoz, 1917).*

M. ["*Agamofilaria*"] *streptocerca* Macfie and Corson, 1922.

M. [*Filaria*] *malayi* Brug, 1927.

Among forms recorded from domestic animals the following may be mentioned:

In the horse:

"*M. sanguinis equi africani*" (Martini, 1903).

In the ox:

M. guyanensis Leger, 1901.

In the dog:

M. auquieri Foley, 1921.

M. lewisii Korke, 1924.

In the fowl:

M. sequini Mathis and Leger, 1909.

PHILOMETRIDÆ.

The family **Philometridæ**† contains certain aberrant forms, rather doubtfully belonging to the Filarioidea, and having the following characters in common:

Body more or less elongated. Anterior end rounded, sometimes with a cuticular shield. Mouth simple, without lip-like structures, but surrounded by six or eight papillæ. Anus sometimes absent in adult. Male, when known, much smaller than female. Spicules two, equal, slender, finely pointed. An accessory piece present. Vulva very inconspicuous or absent, and vagina rudimentary or absent, in gravid

* The vector of this species is said to be *Stegomyia calopus*. It has been suggested by Brumpt that its adult form may be the *Filaria* sp. of Parodi and Bonavia, 1920, of which the female, found in the conjunctiva of a woman in the Argentine, measured 110 mm. in length and 0.41 mm. in thickness, and had the vulva situated at 0.5 mm. from the anterior end. Vogel, as the result of a morphological comparison of the microfilariae, concludes that *M. tucumana* is probably identical with *F. demarquayi* Manson (i.e., *F. ozzardi*).

† See Baylis and Daubney, 1926, *Synopsis of the Families and Genera of Nematoda*, p. 208.

females. Uterine branches directly opposed, forming a continuous tube. Ovaries relatively very short, situated at opposite ends of the body. Viviparous. Adults in body-cavity, serous membranes or connective tissue of vertebrates.

To this family is referred the genus *Dracunculus** Reichard, 1759, including *D. medinensis* (Linnaeus, 1758) (the notorious "Guinea-worm," and the reputed "fiery serpent" of the Children of Israel in the wilderness). The hosts of this parasite are said to include not only man, but the ox, horse, dog and various wild animals. It occurs more especially in Arabia, Persia, Turkestan, India and Africa, but is also recorded from South America, the West Indies and Fiji. The adult female is found in the subcutaneous connective tissue, and when gravid draws attention to its presence by the formation of superficial ulcers of the skin, through which the embryos are discharged on contact with water. The male, although at least two observers state that they have seen it, has never been adequately described. According to Charles, it measures up to about 40 mm. According to Leiper, its length is 22 mm.

The female is of great length, varying from about 32 to 120 cm., and is 0.5 to 1.7 mm. thick. The head bears a cuticular thickening or shield. The mouth is surrounded by eight papillæ. The œsophagus is very short. Into its lumen there open by narrow canals a very large dorsal and two small subventral unicellular glands. The intestine is rudimentary and the anus apparently non-functional. The tail has a ventrally curved, pointed, spine-like termination. The body is almost completely filled by the uterus, each branch of which ends in a short ovary, one at the anterior and the other at the posterior end of the body. The vulva is either completely obliterated in the gravid female or, at all events, extremely difficult to detect. In any case, it apparently does not function as a birth-pore, the usually accepted view being that, when the affected part comes in contact with water, the anterior end of the worm is protruded, whereupon a rupture of the uterus occurs and the embryos escape through the mouth, or through an opening in the cuticle near the head.

The embryos measure 0.5 to 0.75 mm. in length and 0.015 to 0.025 mm. in thickness, and have long, slender tails. They depend for their further development upon the presence in the water of certain "water-fleas"

* According to Leiper (1926) this name was not used in a generic sense by post-Linnaean authors until Wiegmann, in 1834, used it for a reptile. Leiper has proposed the name *Fuellebornius* to replace *Dracunculus* for the worm. *Dracunculus*, however, was placed on the "official list" of generic names by the International Commission on Zoological Nomenclature in 1915 (Opinion 66), Leiper having been one of the authorities who recorded their votes in favour of this step. Unless, therefore, the decision of the Commission is reversed, the name must stand.

(*Cyclops coronatus*, *C. bicuspidatus*, *C. quadricornis*). In the absence of *Cyclops*, the larvæ die in water in a short time. On gaining access to the *Cyclops* (probably by being swallowed), they proceed to migrate through the wall of its alimentary canal into the body-cavity. Here they undergo two moults, one on the eighth and one on the tenth day, but do not grow during this period. Infection of the definitive host apparently takes place through swallowing *Cyclops* with drinking-water. The development of the adult worm is believed to take about a year.

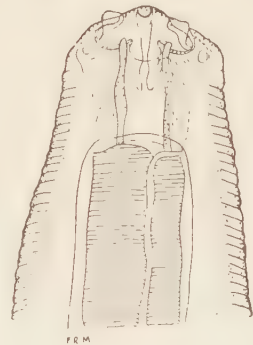
SPIRURIDÆ.

In the family **Spiruridæ** the mouth is bounded by two lateral lips, bearing the cephalic papillæ. A buccal capsule or pharynx is usually present. As in the Filariidæ, the œsophagus is composed of two portions, and the male has two spicules, which are generally unequal and dissimilar. The position of the vulva is very variable, but it is never very close to the anterior end, though it may be in the œsophageal region. The eggs are usually thick-shelled, and contain fully-formed embryos when laid. The adults occur in vertebrates, usually in the alimentary canal or burrowing in its walls, and in those species whose life-histories are known the larvæ are usually found encapsuled in Arthropods.

In the subfamily **Spirurinæ** the lips are followed by a cuticular collar, which is prominent dorsally and ventrally, and may form dorsal and ventral shields overlapping the lips. The buccal capsule is without spiral or annular thickenings. The male typically has four pairs of preanal papillæ, and an accessory piece is usually present.

In this group may be placed the genus **Habronema** Diesing, 1861, three species of which are of common occurrence in the horse, donkey and mule. These worms occur in the stomach (where they often cause the formation of nodules, tumours or ulcers of the wall), and less frequently in the intestine (cæcum and colon). The characters of the genus are as follows:

Cervical alæ may be present. The lips are large and may be entire or trilobed, and sometimes provided with internal teeth. They are overlapped dorsally and ventrally by cuticular shields. A well-developed buccal capsule is present. The male has wide caudal alæ, two to four pairs



100 μ .

FIG. 162.—*Habronema muscæ*:
ANTERIOR END, LATERAL
VIEW. (AFTER RANSOM.)

of pedunculate preanal papillæ and a variable number of postanal papillæ, which are usually asymmetrical in arrangement. The vulva is typically in the middle region of the body. The genus occurs in mammals and birds.

The three species from the horse tribe, with which we are here concerned, may be distinguished as follows:

Habronema muscæ, Carter, 1861. Length, male, 8 to 14 mm.; female, 13 to 22 mm. Buccal capsule cylindrical, 0.048 to 0.059 mm. long. Length of œsophagus 2.3 to 3.5 mm. A lateral ala present on left side of body only. Male with two pairs of preanal papillæ. Left spicule 2.5 mm. long, slender. Right spicule 0.5 mm., much stouter. Tail of female 0.3 to 0.35 mm. long. Vulva very small

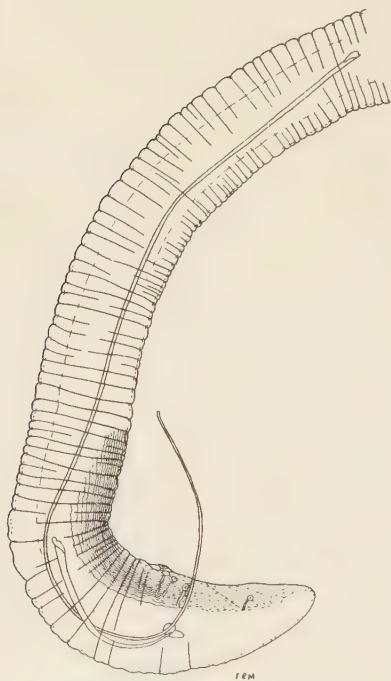


FIG. 163.—*Habronema muscæ*: POSTERIOR END OF MALE, LATERAL VIEW. (AFTER RANSOM.)

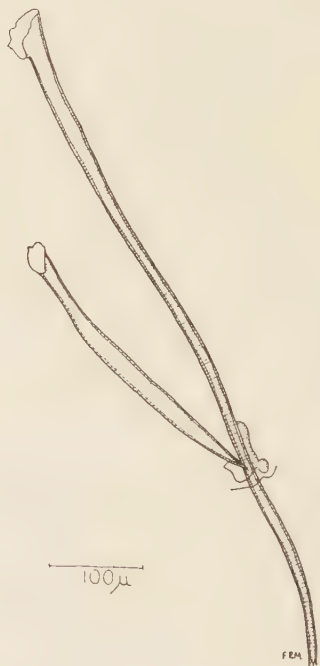


FIG. 164.—*Habronema microstoma*: SPICULES AND ACCESSORY PIECE, VENTRAL VIEW. (AFTER RANSOM.)

and displaced dorsally, the vagina ending in a long, narrow portion without muscular coat, which passes for some distance round the body in the subcuticular layer. Eggs elongate, with thin shells, measuring 0.04 to 0.05×0.01 to 0.012 mm.

H. microstoma (Schneider, 1866). Length, male 9 to 22 mm.; female, 15 to 25 mm. Buccal capsule cylindrical, about 0.075 mm. long.

Length of œsophagus 3 to 3.8 mm. A lateral ala present on left side only. Male with four pairs of preanal papillæ, the left series being in front of the right. Left spicule 0.76 to 0.8 mm. long, right spicule 0.35 to 0.38 mm. Tail of female 0.44 to 0.52 mm. long. Vulva median, ventral. Vagina with large muscular ovejector. Eggs 0.045 to 0.049 $\times$ 0.016 mm., hatching *in utero*.

H. megastoma (Rudolphi, 1819). Differs from the other two species in having the "head" separated by a transverse groove from the "neck," which forms a "shoulder" of thickened cuticle. Length, male, 7 to 10 mm.; female, 10 to 13 mm. Buccal capsule funnel-shaped, about 0.13 mm. long, its wall composed of two separate lateral halves. Male with four pairs of preanal papillæ. Left

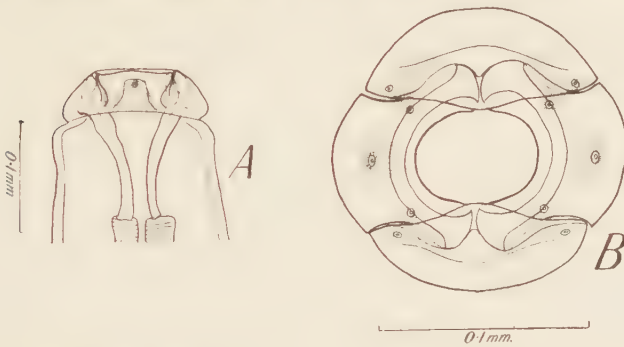


FIG. 165.—*Habronema megastoma*: ANTERIOR END OF FEMALE.
(AFTER BAYLIS AND DAUBNEY.)

A, lateral view; B, *en face* view.

spicule 0.46 mm. long, cylindrical. Right spicule 0.24 mm., flattened and grooved ventrally. Tail of female 0.28 mm. long. Vulva median, ventral. Vagina with small muscular ovejector.

The intermediate hosts of all these species appear to be flies of the genera *Musca* and *Stomoxys*.* The life-history of *H. muscæ*, which has been most completely worked out, is as follows. The embryos, if ingested by the larvæ of the house-fly (*Musca domestica*) or the stable-fly (*Stomoxys calcitrans*) become encapsuled in them, and reach the infective larval stage at about the time when the flies emerge from the pupa. According to Ransom, the chief means by which horses become infected is by swallowing the flies, alive or dead. It appears possible, however, that the larvæ may emerge from the flies when the latter are sucking moisture from the horses' lips or nostrils, or from sores (or, in the case

* Crawford has recorded the infection of a *Drosophilid* fly in Ceylon with larvæ which he believed to belong to *H. megastoma*.

of *Stomoxys*, when biting). Larvæ (the *Dermofilaria irritans* of Rivolta, 1884) found in the "summer sores" of horses have been shown by Railliet and Henry to belong to some undetermined species of *Habronema*. These authors believe them to be the cause of the sores, and to be derived in the first instance from litter soiled with the animals' droppings. It seems conceivable, however, that the sores may be produced first by some other agency, and the worms be deposited in them by flies.

The genus **Parabronema** Baylis, 1921, appears to be very closely related to *Habronema*. It has similar lips and dorsal and ventral

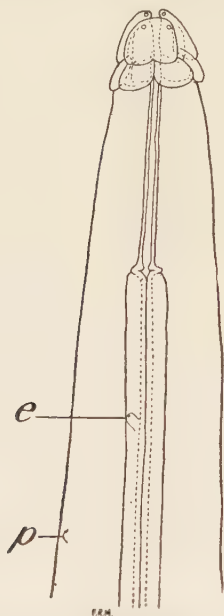


FIG. 166.—*Parabronema skrjabini*:
ANTERIOR END, VENTRAL VIEW.
(AFTER RASOVSKA.)

e., excretory pore; p., cervical papilla.

"shields," but the cuticle of the head is thickened and folded in a complex manner so as to form a circlet of six horseshoe-shaped auricular appendages, of which two are lateral and four submedian. The buccal capsule is elongate, and its posterior portion is cylindrical. The male has four pairs of preanal papillæ and two pairs of postanal papillæ, arranged asymmetrically. There is also a large, double, median, precloacal papilla. The tail of the female is short, bluntly conical, and curved dorsally. The vulva is near the posterior end of the œsophagus.

Four of the five known species of this genus occur in elephants, but one, **P. skrjabini** Rasovska, 1924, is recorded from the stomach of the ox, sheep, goat and camel in Russian Turkestan. The male of this species is 15 to 18 mm. in length, the female up to 36.6 mm. The buccal capsule is 0.13 to 0.22 mm.

long, the œsophagus 2.32 to 2.7 mm. The left spicule measures 0.6 to 0.71 mm., the right spicule 0.29 to 0.31 mm. in length. The tail of the female is 0.29 mm. long, and the vulva is at 5.54 mm. from the anterior end of the body.

The genus **Hartertia** Seurat, 1915, contains rather large, stout worms of somewhat Ascarid-like appearance, parasitic in the intestine of birds and occasionally of mammals. The lips are large and triangular, with a trilobed "pulp" and three internal lobes. A reduced buccal capsule is present. There may be a pair of lateral cervical alæ. The tail of the

male has broad, symmetrical alæ, and there are six pairs of pedunculate caudal papillæ (four preanal and two postanal) and a group of small, sessile papillæ near the tip of the tail. The spicules are very unequal. An accessory piece is present. The vulva of the female is in the middle region of the body.

Hartertia gallinarum (Theiler, 1919) is a form recorded from the small intestine of the fowl in the Orange Free State and in the Belgian Congo. The male measures 28 to 40 mm. in length and about 0.67 to 0.69 mm. in thickness, the female 60 to 110 mm. and about 0.74 to 0.78 mm. respectively. The œsophagus is 3.5 to 6 mm. long. The caudal end of the male is spirally coiled. According to the original description the left spicule measures 0.8 mm. and the right spicule 0.2 mm. in length. Miss Cram, however, who has examined part of the original material, gives the lengths as 2.3 and 0.63 mm. respectively. The left spicule bears four large barbs near the tip, which is sharply pointed. The tip of the right spicule is blunt. The vulva is situated at 16 to 24 mm. from the anterior end. The eggs measure 0.04×0.024 mm.

The life-history of this species has been worked out by Theiler, who finds that the intermediate host is a "white ant" or termite (*Hodotermes pretoriensis*). The worker insects only are infested, not the soldiers. They become infected by ingesting the eggs, and the larvæ develop to the second stage in the abdominal cavity. When the termites are eaten by chickens, the worms reach maturity in three weeks.

Histiocephalus Diesing, 1851, is a remarkable genus occurring beneath the lining of the gizzard of birds. The lips are large, and bear a pair of lateral fringes with a variable number of backwardly-directed processes having simple or subdivided extremities. Dorsal and ventral head-shields are present, as in *Habronema*. The neck region bears an annular swelling composed of a series of longitudinal cuticular folds. The caudal end of the male is spirally coiled and has broad alæ and six pairs of pedunculate papillæ (four preanal and two postanal).

H. laticaudatus (Rudolphi, 1819) occurs in the fowl and duck, and has been recorded from Europe and Asia (Russian Turkestan). In this species the "fringes" have each from ten to twelve processes with from two to four points. The male is 5 to 11 mm. long, the female 7 to 14 mm. The thickness of the body varies between 0.1 and 0.4 mm. The spicules of the male are equal and slender, and relatively very long (6 mm. in a 9.3 mm. specimen). The tail of the female is bluntly conical. The vulva is situated in the anterior region of the body.

In the subfamily **Arduenninæ** the lips, which are not prominent, are trilobed. Dorsal and ventral cuticular shields are absent. In the more

typical genera the buccal capsule or pharynx has annular or spiral thickenings in its walls. There is frequently an asymmetrical development of the cervical alæ, and of the caudal alæ, papillæ and other secondary sexual characters of the male. An accessory piece is present in the male.

The genus *Arduenna* Railliet and Henry, 1911, contains two species parasitic in the stomach of swine. In these forms a cervical ala is present on the left side only. The buccal capsule has well-developed spiral ridges in its wall. The caudal alæ of the male are asymmetrical, and the cloaca is surrounded, at least on the left side and posteriorly, by a cuticular thickening with a serrated margin.

A. strongylina (Rudolphi, 1819) occurs in the stomach and small intestine of the pig and wild boar, and is of wide distribution. It has

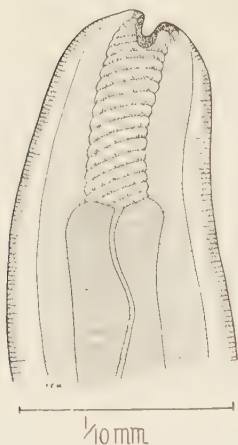


FIG. 167.—*Arduenna strongylina*:
ANTERIOR END. (AFTER
FOSTER.)

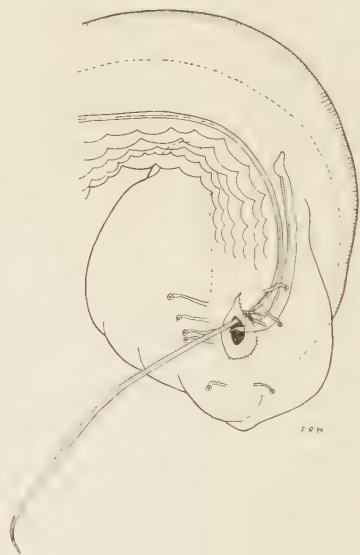


FIG. 168.—*Arduenna strongylina*:
POSTERIOR END OF MALE, VEN-
TRAL VIEW. (AFTER FOSTER.)

been recorded once from the ox in America. The male is 10 to 15 mm. long, the female 16 to 22 mm. The maximum thickness of the body is about 0.3 to 0.39 mm. The buccal capsule is 0.083 to 0.098 mm. long and about 0.029 mm. wide. The length of the œsophagus is 3.1 to 3.7 mm. In the male the right caudal ala is about twice as wide as the left, and the pedunculate caudal papillæ, of which four pairs are preanal and one post-anal, are asymmetrically arranged. The left spicule is slender and measures 2.24 to 2.95 mm. in length. The right spicule is shorter and

measures 0.457 to 0.619 mm. The tail is 0.155 to 0.2 mm. long. In the female the bluntly conical tail measures 0.215 to 0.275 mm. in length, and the vulva is situated a little in front of the middle of the body and is displaced towards the left side, near the lateral ala. The eggs are oval, with thick shells, surrounded by a thin membrane and measuring 0.034 to 0.039 $\times$ 0.02 mm. The intermediate hosts are coprophagous beetles of the genera *Onthophagus* and *Aphodius* (*O. hecate*, *A. castaneus*, *A. rufus*).

Arduenna dentata (v. Linstow, 1904) is a larger species occurring in the domestic pig and in *Sus cristatus* in Indo-China and the Malay region. The male measures about 25 mm. in length and 0.79 mm. in thickness, the female 55 and 1.1 mm. respectively. According to v. Linstow the longer spicule measures 0.92 mm. and the shorter 0.35 mm. According to Railliet and Henry the lengths of the spicules are 3.75 to 4.23 mm. and 0.54 to 0.65 mm. respectively. The caudal papillæ are as in *A. strongylina*. The vulva of the female is considerably behind the middle of the body. The eggs are cylindrical, and measure 0.039 $\times$ 0.017 mm.

Simondsia paradoxa Cobbold, 1864, is a remarkable form found in the stomach of the pig in Europe. The male is slender and 12 to 15 mm. long, and occurs free in the lumen of the stomach or partly buried in the mucosa. The female, when gravid, is about 15 mm. long, and has the posterior portion of the body enlarged into a more or less globular sac. It occurs in small tumours or cysts in the stomach-wall, from which its slender anterior end is protruded. Lateral cervical alæ are present. Within the opening of the mouth are a large dorsal and a large ventral tooth. The buccal capsule is long and cylindrical, and has spiral thickenings in its wall. The caudal end of the male is spirally coiled. According to Cobbold there are two spicules, which are unequal, long and slender. According to Colucci and Arnone there is a single spicule. The female has the vulva situated in the anterior third of the body, on the slender portion. The eggs are oval or ellipsoidal, and measure 0.028 to 0.029 mm. in length.

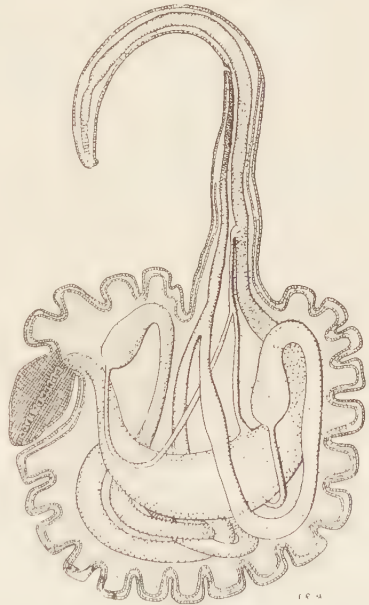


FIG. 169.—*Simondsia paradoxa*: FEMALE, IN OPTICAL SECTION. (FROM HALL, AFTER COLUCCI AND ARNONE.)

In the genus **Physocephalus** Diesing, 1861, the cuticle of the anterior extremity is inflated, and there are three parallel lateral alæ on each side of the body. The oral cavity is small and without teeth, but there is a large buccal capsule, with spiral and annular thickenings. The caudal end of the male is spirally coiled, and has narrow, symmetrical alæ. The vulva is behind the middle of the body.

P. sexalatus (Molin, 1860) occurs in the stomach and small intestine of the pig, wild boar and peccary, and is of wide distribution. It has also been recorded from the tapir, donkey and camel, and from the ox in America. The male is 6 to 13 mm. long, the female 13 to 22.5 mm. The maximum thickness is a little over 0.3 mm. in the male, 0.33 to

0.45 mm. in the female. The cephalic cuticular inflation extends for a distance of about 0.23 mm. The buccal capsule is about 0.265 mm. long and 0.053 mm. wide. The male has four pairs of pedunculate preanal papillæ and four pairs of shorter postanal papillæ, the latter situated near the tip of the tail. The spicules are alate and sharply pointed, the left measuring 2.1 to 2.5 mm., the right 0.3 to 0.4 mm. in length. The tail of the female is 0.12 mm. long, and is blunt, but with a mucronate tip. The eggs are ellipsoidal and slightly flattened at the poles. The shell is surrounded by a thin membrane and measures 0.034 to 0.039 $\times$ 0.015 to 0.017 mm. The larvæ occur in coprophagous beetles, includ-

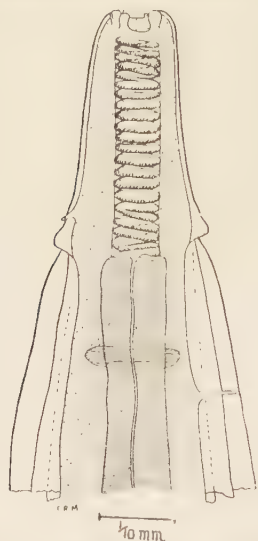


FIG. 170.—*Physocephalus sexalatus*:
ANTERIOR END, DORSAL VIEW.
(AFTER FOSTER.)

ing *Scarabæus* (*Ateuchus*) *sacer*, *S. variolosus*, *Gymnopleurus sturmi*, *Geotrupes douci*, *Onthophagus nebulosus* and *O. bedeli*. The third-stage larvæ are also found encapsuled in various small vertebrates (amphibia, reptiles, birds and mammals) which have, presumably, fed upon the beetles.

Physocephalus cristatus (Seurat, 1912) Railliet, 1915, is a form originally described by Seurat as a variety of *P. sexalatus*, existing side by side with it in the camel, but regarded by Railliet as a distinct species. The head bears four longitudinal crests or folds, corresponding to four cuticular ridges in the buccal cavity. The posterior end of the male is not spirally coiled, but the whole body is twisted about its axis through an angle of 180°. The spicules measure 2.5 and 0.3 mm. respectively. The position of the vulva is very variable.

In *Spirocerca* Railliet and Henry, 1911, the buccal capsule is short and expanded in its anterior portion, and its walls are without local thickenings. The male has narrow caudal alæ, and the caudal papillæ consist of four preanal pairs, a large median papilla on the anterior lip

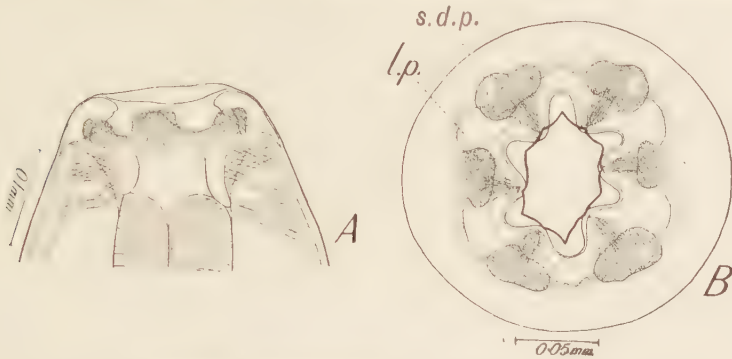


FIG. 171.—*Spirocerca sanguinolenta*: ANTERIOR END OF FEMALE. (AFTER BAYLIS.)

A, lateral view; B, en face view; l.p., lateral papilla; s.d.p., subdorsal papilla.

of the cloaca, two pairs of large postanal papillæ and a group of four or five pairs of minute papillæ near the tip of the tail.

S. sanguinolenta (Rudolphi, 1819) occurs in the dog, and also in the wolf, jackal and fox, and is common in most warm countries, including

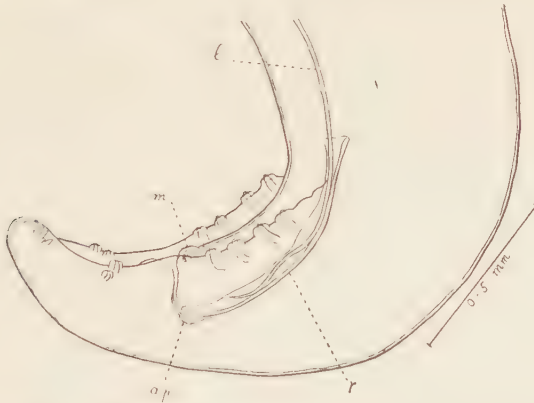


FIG. 172.—*Spirocerca sanguinolenta*: POSTERIOR END OF MALE, LATERAL VIEW. (AFTER BAYLIS.)

a.p., accessory piece; l., left spicule; m., median preanal papilla; r., right spicule.

the South of Europe. The cat does not seem to be naturally infected, but has been found to be susceptible of experimental infection. The worms inhabit tumours in the walls of the stomach and œsophagus, and also sometimes in the lymphatic glands, bronchi, thoracic and abdominal

cavities, and in the wall of the aorta. They are usually blood-red when fresh. The male measures 30 to 54 mm. in length and up to 0.76 mm. in thickness, the female 54 to 80 mm. and 1.15 mm. respectively. There are six small papillæ within the opening of the mouth. The buccal cavity is about 0.09 to 0.1 mm. in length and about the same in width anteriorly, but narrower posteriorly. It contains no teeth. The œsophagus is about 5.8 mm. long in the male, 7 mm. in the female. The left spicule of the male is about 2.45 mm. long, the right 0.75 mm. In the female the tail is 0.4 to 0.45 mm. long, and is usually curved dorsally. The vulva is variable in position, being sometimes in front of, and sometimes behind, the posterior end of the œsophagus. The eggs are cylindrical and measure about 0.0375×0.015 mm.

The intermediate hosts of this species are various coprophagous beetles, including *Scarabæus* (*Ateuchus*) *sacer*, *S. variolosus*, *Akis goryi*, *Geotrupes douei*, *Copris hispana* and *Gymnopleurus sturmi*. The third-stage larvæ also occur encapsuled in numerous amphibia, reptiles, birds (including the fowl and sparrow), and small mammals (including mice, rats and hedgehogs).

Infection-experiments carried out by Faust on dogs and cats, with larvæ from the mesentery and omentum of a hedgehog (*Erinaceus dealbatus*), indicate that the larvæ do not penetrate directly into the œsophageal wall, but that they have a complex route of migration. Apparently they leave their cysts in the stomach and, passing through its wall, travel by way of the portal system and the capillaries of the lungs into the arterial system, in the walls of which the primary lesions occur. Some of the worms in the aorta may penetrate through the adjacent tissues and thus reach the wall of the œsophagus. The eggs, apparently, can only reach the exterior when the tumours containing the adult worms have acquired an opening into the lumen of the alimentary canal.

Spirocerea arctica Petrov, 1927, is a much smaller form occurring in the dog and Arctic fox (*Vulpes lagopus*) in North Russia, in tumours of the stomach-wall. The male is about 6.2 to 6.8 mm. long, the female 9.5 to 12.5 mm. The pharynx is about 0.055 mm. long and 0.028 mm. wide, and contains six pointed and forwardly-directed teeth. The left spicule of the male is about 0.83 to 0.84 mm. long, the right spicule 0.293 to 0.296 mm. The tail of the female measures 0.152 to 0.172 mm., and the vulva is only slightly in front of the middle of the body. The eggs are oval, and measure 0.035 to 0.039×0.019 to 0.023 mm.

Cylicospirura Vevers, 1923, is a genus very closely resembling *Spirocerea*, from which, however, it differs in having six protrusible bicuspid or tricuspid teeth at the entrance to the buccal capsule.

C. subæqualis (Molin, 1860) occurs in the stomach of various wild Felidæ, and has also been recorded by Chandler (under the name of *Spirocerca felineus*) from the domestic cat in India. The male is about 18 to 22 mm. long and 0.48 to 0.54 mm. thick, the female 19 to 30 mm. and 0.9 mm. respectively. The buccal capsule is expanded anteriorly and measures 0.105 to 0.14 mm. in length. The œsophagus is 4.2 to 5.3 mm. long. The caudal papillæ of the male are as in *Spirocerca*. The left spicule measures 2.25 to 2.5 mm., the right about 0.5 mm. The vulva is situated at 3 to 5 mm. from the anterior end. The eggs measure 0.037 to 0.039 $\times$ 0.016 to 0.018 mm.

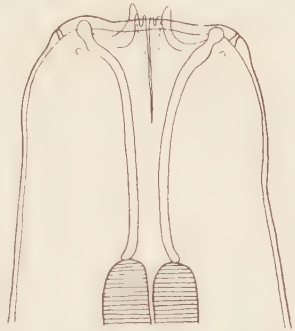


FIG. 173.—*Cylicospirura subæqualis*:
ANTERIOR END, VENTRAL VIEW.
(AFTER YORKE AND MAPLE-
STONE.)

The genus **Gongylonema** Molin, 1857, shows certain affinities with the Arduenninæ. In this genus the lips are very small and inconspicuous, but form a minute, funnel-like border surrounding the mouth. A short pharynx is present. The anterior portion of the body, at least on the left side, bears a number of rounded or oval cuticular elevations or bosses, arranged, as a rule, in irregular longitudinal rows. Cervical alæ are present, or at least a single ala on the left side. The caudal alæ of the male are asymmetrical, and there is a variable number of pairs of pedunculate preanal and postanal papillæ. The vulva of the female is situated towards the posterior end of the body. The adults occur in galleries in the mucous membrane of the œsophagus, mouth or stomach of mammals, or of the crop of birds.

Gongylonema pulchrum Molin, 1857. The following are, in the writer's opinion, synonyms of this species: *Spiroptera scutata* Müller, 1869; *Gongylonema confusum* Sonsino, 1896; *G. ransomi* Chapin, 1922; *Filaria labialis* Pane, 1864; *Gongylonema subtile* Alessandrini, 1914; *G. hominis* Stiles, 1921.

This form occurs in the pig, sheep, goat, ox, zebu and buffalo, and has also been recorded as an occasional parasite of the horse, donkey, camel, wild boar and man. It has been transmitted experimentally to the rat. Its habitat is chiefly the lining of the œsophagus, but in ruminants it sometimes occurs also in the rumen. It is recorded from Eastern and Southern Europe, India, Africa, America and Australia.

The male measures up to 62 mm. in length and 0.15 to 0.3 mm. in thickness. The female attains a length of 145 mm. and a thickness of 0.5 mm. The anterior end is covered on both sides with bosses, which

are usually arranged in two main rows in each of the four submedian fields. The cervical alæ are symmetrical and relatively broad. The pharynx is 0.04 to 0.08 mm. long, the œsophagus about 3 to 9 mm. The tail of the male measures 0.22 to 0.35 mm. in length. The preanal papillæ have long peduncles and are very variable in number and often asymmetrical. Most commonly there are five pairs. The postanal papillæ consist of four pairs of pedunculate papillæ and a group of about four pairs of very small, sessile papillæ near the tip of the tail. The left spicule is slender and extremely variable in length (4 to 23 mm.). The

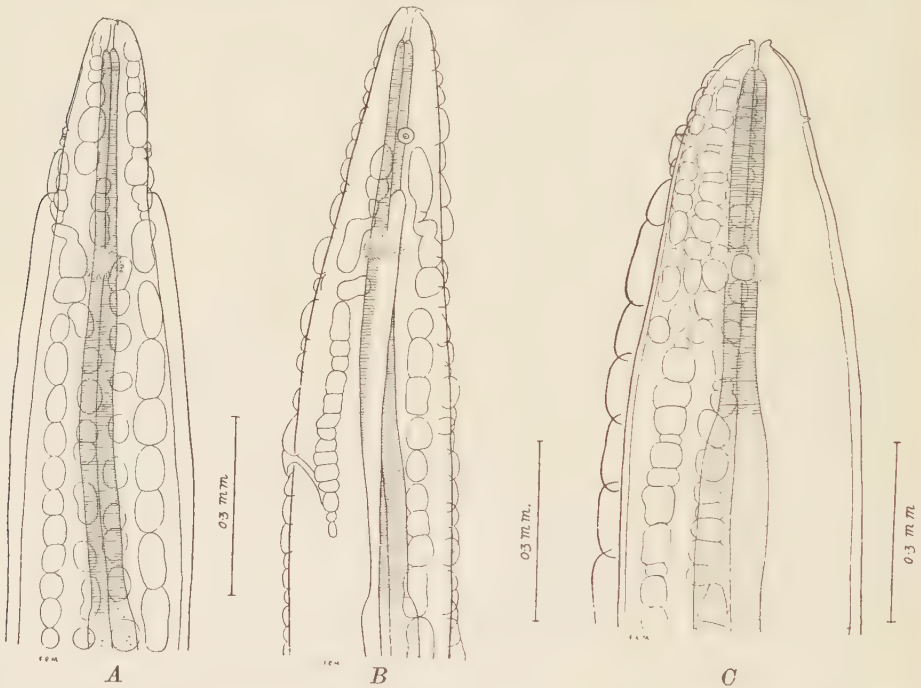


FIG. 174.—(A), *Gongylonema pulchrum*, ANTERIOR END, DORSAL VIEW; (B), THE SAME, LATERAL VIEW; (C), *Gongylonema verrucosum*, ANTERIOR END, DORSAL VIEW. (AFTER BAYLIS.)

right spicule is much stouter and measures 0.084 to 0.18 mm. The accessory piece is 0.07 to 0.12 mm. long. The tail of the female is bluntly conical. The vulva is situated at a very variable distance (about 2 to 7 mm.) from the posterior end. The eggs measure 0.05 to 0.07 × 0.025 to 0.037 mm.

The larvæ of this species occur encapsuled in various coprophagous beetles. Ransom and Hall found them in the United States in *Aphodius femoralis*, *A. granarius*, *A. fimetarius*, *A. coloradensis*, *A. vittatus*, *Onthophagus hecate* and *O. pennsylvanicus*. In Italy, the present writer has

found them in *Onthophagus taurus*, *Caccobius schreberi*, *Aphodius hæmorrhoidalis* and *Oniticellus fulvus*.* The small "German" cockroach, *Blattella germanica*, is also readily infected under experimental conditions. Infection of the definitive hosts presumably occurs normally through the accidental or purposive ingestion of the intermediate hosts. Certain experiments of the writer's have shown that if the insect host should fall into water, the contained infective larvæ may emerge from its body and continue to live for some time in the water. As they do not swim, but sink to the bottom, it is unlikely that they would usually be taken up by animals drinking from a water-supply thus contaminated, unless it were



FIG. 175.—POSTERIOR END OF MALE, VENTRAL VIEW, OF (A), *Gongylonema pulchrum*; (B), *G. monnigi*; (C), *G. verrucosum*. (AFTER BAYLIS.)

a.p., accessory piece; l.s., left spicule; r.s., right spicule.

very shallow. There seems, however, to be a possibility of water occasionally playing a part in the transmission of *Gongylonema*.

Gongylonema verrucosum (Giles, 1892) (= *crenatum* Railliet, 1898) occurs in the rumen of the sheep, ox and zebu in India and South Africa. It is peculiar in having a single, broad, festooned, cervical ala on the left side only, and in having the cuticular bosses confined to the left side

* Seurat, in Algeria, records this species from certain beetles of the genus *Blaps*, but the larvæ referred to seem more probably to have belonged to another species. On the other hand, larvæ found by Seurat in *Scarabæus* (*Ateuchus*) *sacer*, *Onitis irroratus*, *Onthophagus bedeli*, *Geotrupes douei*, *Gymnopleurus mopsus* and *G. sturmi*, though referred by him to another species, very probably belonged to *G. pulchrum*.

of the middle line. The male is 32 to 41 mm. long and 0.25 to 0.3 mm. thick, the female 70 to 95 and 0.42 to 0.46 mm. respectively. Other measurements are: Length of pharynx, 0.04 to 0.05 mm.; œsophagus, male, 6.5 to 8.5 mm., female, 8 to 10 mm.; tail of male, 0.28 to 0.38 mm.; left spicule, 9.5 to 10.5 mm.; right spicule, 0.26 to 0.32 mm.; accessory piece, 0.13 to 0.16 mm.; tail of female, 0.3 mm.; vulva from posterior end, 1.2 to 3.2 mm.; eggs 0.045 to 0.055 $\times$ 0.025 to 0.032 mm. The male has five to eight preanal papillæ on either side (frequently asymmetrical), four postanal papillæ on the left and three to five on the right side.

G. monnigi Baylis, 1926, occurs in the rumen of the sheep in South Africa. It has a single, narrow cervical ala, which is not festooned, on the left side. The cuticular bosses are similar to those of *G. verrucosum*, but less strictly confined to the left side.

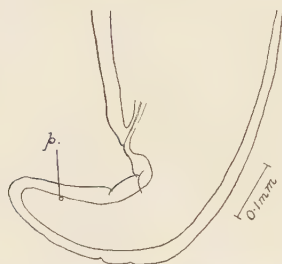


FIG. 176.—*Gongylonema monnigi*:
POSTERIOR END OF FEMALE,
LATERAL VIEW. (AFTER BAYLIS.)
p., caudal papilla.

Measurements: Length, male, 42 mm., female, 102 to 113 mm.; maximum thickness, male, 0.3 mm., female, 0.43 to 0.45 mm.; length of pharynx, 0.045 to 0.055 mm.; œsophagus, 9 to 12 mm.; tail of male, 0.35 mm.; left spicule, about 15 mm.; right spicule, 0.26 mm.; accessory piece, 0.15 mm.; tail of female (bent ventrally almost at a right angle), 0.2 to 0.3 mm.;

vulva from posterior end, 4 to 6 mm.; eggs, 0.06 to 0.0625 $\times$ 0.035 to 0.0375 mm. The male has ten or eleven pairs of caudal papillæ, of which seven pairs are preanal.

G. ingluvicola Ransom, 1904, occurs in the lining of the crop of the fowl, and is recorded from North America, the Philippines, Roumania, Formosa and Australia. The cervical alæ of this species are narrow and symmetrical, and the cuticular bosses are very closely apposed posteriorly. Measurements: Length, male, 17 to 20 mm., female, 32 to 55 mm.; maximum thickness, male, about 0.25 mm., female, 0.32 to 0.49 mm.; length of pharynx, 0.032 to 0.04 mm.; œsophagus, about 3.4 to 3.7 mm. in male, 5.5 to 6.5 mm. in female; tail of male, 0.225 to 0.275 mm.; left spicule, 17 to 19 mm. (being of about the same length as the body, this is folded when retracted); right spicule, 0.1 to 0.12 mm.; tail of female, 0.165 to 0.288 mm.; vulva from posterior end, 2.5 to 3.5 mm.; eggs, 0.05 to 0.057 $\times$ 0.036 to 0.038 mm. The caudal papillæ of the male are very variable and asymmetrical. There are up to seven preanal papillæ, and up to five postanal, on each side.

In the subfamily **Acuariinæ** the lips are simple, conical and distinct, though usually very small. The cuticle of the anterior end of the body is provided with ornamentations in the form either of "cordons" (as they have been termed by French authors)—which are grooves, tubular channels or festoon-like bands, sometimes of complex structure—or of "epaulettes" or projecting lappets, sometimes forming a complete cuticular collar. The worms are generally slender and very translucent, and occur beneath the cuticular lining of the gizzard, or in the walls of the œsophagus and crop, or "stomach," of birds. The buccal capsule is cylindrical and thin-walled, without thickenings. The males typically possess four pairs of preanal papillæ and are without an accessory piece.

In the genus **Acuaria** Bremser, 1811 (= *Anthuris* Rudolphi, 1819; *Spiroptera* Rudolphi, 1819; *Dispharagus* Dujardin, 1845) the anterior end bears four "cordons" which may be prominent or sunk in the cuticle. These cordons may run straight backwards from the lips and terminate separately, or, more often, turn forward again and either terminate separately or join in pairs across the lateral fields. According to the arrangement of the cordons, and the number of postanal papillæ and form of the spicules in the male, the genus may be divided into a number of subgenera. The forms occurring in domestic poultry fall into three of these groups (*Cheilospirura*, *Dispharynx* and *Echinuria*).

The subgenus **Cheilospirura** Diesing, 1861, has "cordons" which run straight posteriorly and are non-recurrent and not anastomosed. There are five to seven pairs of postanal papillæ in the male, and the spicules are very unequal and dissimilar. To this group belongs **Acuaria hamulosa** (Diesing, 1851), a cosmopolitan parasite of the fowl and turkey, in which birds it occurs in small nodules in the wall of the gizzard. The male of this species is 8.5 to 14 mm. in length and 0.3 mm. in thickness. Its tail measures 0.6 to 0.7 mm., and bears some six pairs of postanal papillæ. The left spicule

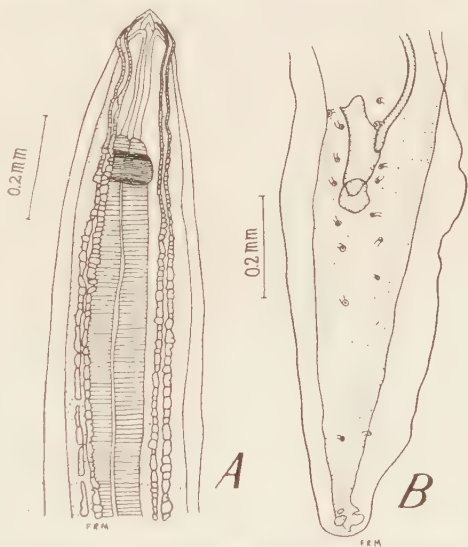


FIG. 177. —*Acuaria* (*Cheilospirura*) *hamulosa*. (AFTER TUBANGUI.)

A, anterior end, lateral view; B, posterior end of male, ventral view.

is slender and about 1.8 mm. long, the right broad and flattened, and 0.5 mm. long. The female measures 16 to 25 mm. in length and 0.5 mm. in thickness, and has a tail 0.5 to 0.6 mm. long. The vulva is situated a little behind the middle of the body, and the eggs measure 0.043 to 0.045×0.024 to 0.025 mm.

In the subgenus **Dispharynx** Railliet, Henry and Sisoff, 1912, the "cordons" are recurrent but not anastomosed. There are usually five pairs of postanal papillæ in the male, and the spicules are unequal and dissimilar.

Acuaria (Dispharynx) spiralis (Molin, 1858) occurs in the mucosa of the œsophagus, crop and intestine of the fowl, turkey, guinea-fowl, pigeon,

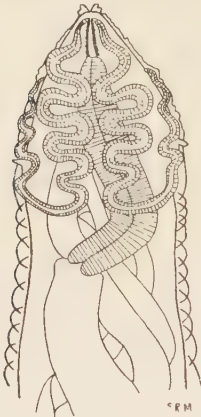


FIG. 178.—*Acuaria (Dispharynx) spiralis*: ANTERIOR END, VENTRAL VIEW. (AFTER TUBANGUI.)

pheasant and various other birds, and is of world-wide distribution. The male is 4.5 to 8.3 mm. long and 0.23 to 0.5 mm. thick. The caudal end is spirally coiled, and the tail is 0.275 to 0.34 mm. long. The left spicule is slender and 0.4 to 0.52 mm. in length, the right spicule broad and boat-shaped and 0.15 to 0.2 mm. long. The female measures 5.5 to 10.2 mm. in length and 0.36 to 0.57 mm. in thickness. Its tail is 0.11 to 0.13 mm. long, and ends in a small spike. The eggs measure 0.033 to 0.04×0.018 to 0.025 mm.

Piana found larvæ which he attributed to *A. nasuta*, but which probably belonged to this species, in woodlice (*Porcellio laevis*). Infection of the definitive hosts is therefore probably acquired by swallowing these crustaceans.

A second species, **A. (Dispharynx) nasuta** (Rudolphi, 1819) is said to occur in the fowl, but, although it was taken by Railliet, Henry and Sisoff as the type of the subgenus, it is a very imperfectly-described form, and it seems quite possible that it is really identical with *A. spiralis*. The vulva, in both species, is variously stated by different describers to be in the anterior or in the posterior half of the body, and its position appears, therefore, to be subject to a good deal of variation.

In the subgenus **Echinuria** Soloviev, 1912, the "cordons" are non-recurrent, but are anastomosed in pairs. The body is sometimes spiny. The male has four or five pairs of postanal papillæ, and unequal and dissimilar spicules.

Acuaria (Echinuria) uncinata (Rudolphi, 1819) is a parasite of the duck, goose, swan and certain related wild birds. It inhabits the mucosa of the œsophagus, glandular stomach and small intestine, and is found in Europe, North Africa and North America. The cuticle of the body bears four longitudinal rows of spines throughout almost its entire length. The male is 8 to 10 mm. long and 0.3 to 0.5 mm. thick, the female 12 to 18.5 and 0.515 mm. respectively. The tail of the male measures 0.33 mm., and the lengths of the spicules are 0.706 and 0.208 mm. The tail of the female is 0.25 mm. long, and the vulva is situated at 1 to 1.4 mm. from the posterior end. The eggs measure 0.037×0.02 mm.

According to Hamann, the water-flea *Daphnia pulex* acts as an intermediate host for this species.

A. (Echinuria) jugadornata Soloviev, 1912, recorded from the duck in Russian Turkestan, appears to be somewhat doubtfully distinct from the last-mentioned form. The lengths of the spicules are given as 0.839 and 0.14 mm. respectively, and the worms appear to be a little larger and stouter, but there is little else in the description to suggest that the species are not identical.

In the genus **Streptocara** Railliet, Henry and Sisoff, 1912, the anterior end is surrounded by a delicate cuticular collar with its free edge directed posteriorly and denticulate or festooned. In other respects the species closely resemble those of *Acuaria*. They occur chiefly in fish-eating birds, but one species, **S. pectinifera** (Neumann, 1900) is a parasite of the fowl and guinea-fowl, occurring beneath the lining of the gizzard. The male of this species measures 4 to 5.2 mm. in length and 0.15 to 0.176 mm. in thickness, the female 6.5 to 9.6 and 0.275 to 0.28 mm. respectively. The cervical papillæ form semilunar cuticular "epaulettes," each with from five to seven denticulations on its posterior edge. The œsophagus is about 2 mm. long. The male has four pairs of pre-anal and five pairs of postanal papillæ, the latter gradually diminishing in length posteriorly. The left spicule is 0.265 to 0.3 mm. long, the right (which is stouter) 0.075 to 0.088 mm. Both spicules are barbed at their tips. The vulva is slightly behind



FIG. 179.—*Streptocara pectinifera* : POSTERIOR END OF MALE, VENTRAL VIEW. (AFTER NEUMANN, MODIFIED.)

the middle of the body. The eggs measure 0.033 to 0.039×0.02 to 0.021 mm.

Probably closely related to the *Acuariinæ* is the remarkable genus ***Tropisurus*** Diesing, 1835 (= *Tetrameres* Creplin, 1846; *Tropidocerca* Diesing, 1851; *Acanthophorus* v. Linstow, 1876). The worms of this genus occur in the glandular stomach or crop of birds, the males being found free in the lumen, while the females, which are often blood-red in colour, are partly buried in the gastric glands, with their posterior ends protruding. The lips of these worms are small and inconspicuous. There is a short, cylindrical buccal capsule. The male is slender, and its cuticle is usually armed with four longitudinal rows of spines. The

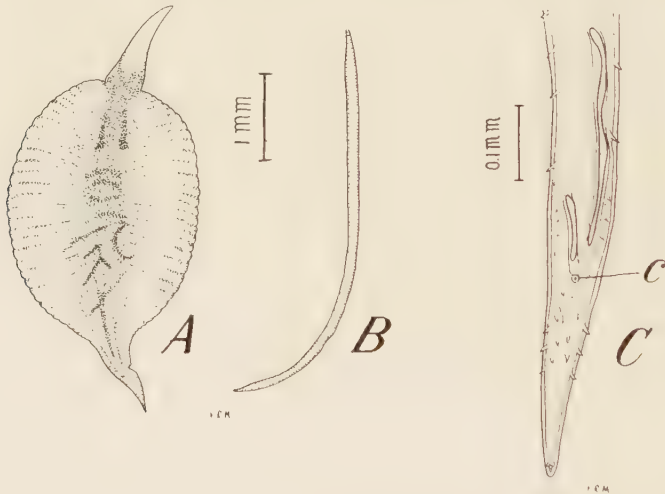


FIG. 180.—*Tropisurus fissispinus*. (AFTER TUBANGUI.)

A, female; B, male; C, posterior end of male, ventral view; c., cloacal aperture.

caudal end is without alæ, and the papillæ are few, small and sessile. The spicules are very unequal. The middle portion of the body of the gravid female becomes enormously distended by the contents of the uterus, so as to assume a fusiform or subglobular shape, divided into quarters by four longitudinal grooves in the lateral and median lines, while the œsophageal and caudal regions remain normal. The intestine of the female is wide and sac-like.

Tropisurus fissispinus (Diesing, 1861) (= *Tropidocerca fissispina* Dies., 1861; *Acanthophorus tenuis* v. Linstow, 1876; *A. horridus* v. Linst., 1876; *Filaria pulicis* v. Linst., 1894) occurs in the duck, pigeon, fowl, turkey and various wild aquatic birds, and is of wide distribution. The male measures 3 to 6 mm. in length and 0.09 to 0.2 mm. in thickness. The tail

is 0.13 to 0.25 mm. long. The spicules measure respectively 0.082 to 0.15 mm. and 0.28 to 0.49 mm. The female is 1.67 to 6 mm. long and 1 to 3.5 mm. thick. The tail is 0.07 to 0.2 mm. long, and the vulva is situated at 0.31 mm. from the posterior end. The eggs measure 0.048 to 0.056 $\times$ 0.026 to 0.03 mm.

The fresh-water crustacea *Daphnia pulex* and *Gammarus pulex* are apparently capable of acting as intermediate hosts for this species, the larvæ developing in their body-cavities.

Tropisurus confusus (Travassos, 1919) (= *Tetrameres travassosi* Skrjabin, 1920) occurs in the crop of the pigeon, fowl and turkey in Brazil. The male is 4 to 5 mm. long, the female 3 to 5 mm. The spicules measure 0.068 and 0.291 mm. The tail of the male is 0.07 mm. long, and ends in a small hook. The tail of the female measures 0.25 mm., and the vulva is close to the anus. The eggs measure 0.033 $\times$ 0.024 mm.

T. gigas (Travassos, 1919) is recorded from the glandular stomach of the duck in Brazil. The male is 7.5 mm. long and 0.18 mm. thick, and its tail is 0.12 mm. long and curved dorsally. The spicules measure 0.016 and 0.74 mm. The female measures 5 to 6 mm. in length and 4 to 5 mm. in thickness. The cuticle is conspicuously transversely striated anteriorly. The eggs measure 0.05 $\times$ 0.021 mm.

T. americanus (Cram, 1927) occurs in the crop of the fowl in the United States. The male is 5 to 5.5 mm. long and 0.116 to 0.133 mm. thick, and has two double submedian rows of spines. The tail is 0.232 to 0.29 mm. long, and the spicules measure respectively 0.1 and 0.29 to 0.312 mm. The female measures 3.5 to 4.5 mm. in length and 3 mm. in thickness. The tail is 0.332 mm. long, and the vulva is situated at 0.631 to 0.664 mm. from the posterior end. The eggs measure 0.042 to 0.05 $\times$ 0.025 mm.

A species from the fowl in Formosa appears to have been described by Sugimoto in 1923 under the name of *T. gallineis*. The description of this form is not accessible to the writer.

Tropisurus (*Microtetrameres*) *inflatus* (Mehlis, in Creplin, 1846), recorded from the duck, is so imperfectly described that its status is very doubtful. Miss Cram, who has recently investigated all the available evidence, concludes that the worm in question was probably *Eustrongylides mergorum* (Rudolphi, 1809), a form with somewhat similar habits to those of *Tropisurus*, and occurring in various aquatic birds. This, however, does not seem to have been met with again in the domestic duck.

In the subfamily **Physalopterinae** the lips are simple and relatively large, provided with forwardly-directed teeth on their inner surfaces and frequently followed by a collar-like fold of cuticle, within which

they may be more or less retractile. There is no buccal capsule or pharynx.

Physaloptera Rudolphi, 1819 (including *Chlamydonema* Hegt, 1910), is a genus with a large number of species occurring in the alimentary canal (generally in the stomach) of mammals, birds, reptiles and, rarely, amphibians. In this genus each lip is armed with a variable number of teeth. Typically there is a large, external, median "tooth" or conical

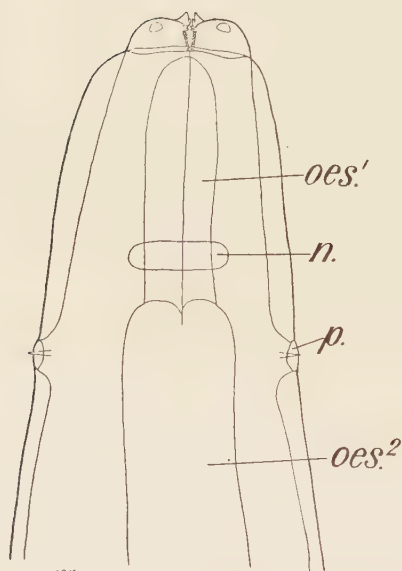


FIG. 181. — *Physaloptera caucasica*: ANTERIOR END OF FEMALE. (AFTER SCHULZ.)

n., nerve-ring; *oes.*¹, *oes.*², anterior and posterior portions of œsophagus; *p.*, cervical papilla.



FIG. 182. — *Physaloptera caucasica*: POSTERIOR END OF MALE, VENTRAL VIEW. (AFTER SCHULZ, MODIFIED.)

l., left spicule.

process, and a group of three internal teeth. There may, in addition, be a series of small denticles on the inner surface. The head is usually more or less retractile within a cuticular collar. The caudal end of the male is provided with well-developed and swollen lateral alæ which are joined across the ventral surface in front of the cloaca, and thus form a bursa-like structure. The ventral surface of this is usually largely covered with small cuticular elevations. In the cloacal region there are at least four pairs of ray-like lateral papillæ with long peduncles. There

are also several pairs of sessile median and subventral papillæ (usually three preanal and five pairs postanal). The spicules may be unequal, subequal, or equal. The uterus of the female shows various modifications of the typical two-branched form, having in some species four branches, arising either together or by dichotomous branching from the main trunk, and in other species more numerous branches.

Nothing is yet known of the life-history of any species of *Physaloptera*, though it is to be presumed that an intermediate host, probably an insect or other invertebrate, is required for the development of the larvæ. Six species of this genus have been recorded as parasites of man and domestic animals.

Physaloptera caucasica v. Linstow, 1902 (= *P. mordens* Leiper, 1908), was originally recorded from man in the Caucasus, and has since been found in man in Central Africa and also in African monkeys. The male of this species measures 14.2 to 34 mm. in length and 0.7 to 1 mm. in thickness; the female 22 to 100 and 1.1 to 2.8 mm. respectively. The lips have a large external tooth and a single small median internal tooth. Near the dorsal and ventral edges of each lip there is a bifid tooth, and between these and the median tooth, and also dorsally and ventrally to them, there are irregular rows of small denticles. The left spicule of the male is filiform and measures 3.2 to 5.5 mm. in length. The right spicule is broader and measures 0.47 to 0.5 mm., according to Ortlepp.* The arrangement of the caudal papillæ is shown in Fig. 182. The vulva of the female is situated near (a little behind or in front of) the posterior end of the œsophagus, and is slightly prominent. The uterus has four branches, which arise dichotomously. The oval, thick-shelled eggs measure 0.045 to 0.062 $\times$ 0.032 to 0.045 mm.

Physaloptera præputialis v. Linstow, 1889 (= *Chlamydonema felineum* Hegt, 1910), occurs in the stomach of the cat, and also of the leopard and various other wild Felidæ, in the East Indies, Africa and South America. According to Chandler, who found this parasite in about 2 per cent. of the domestic cats examined by him in Calcutta, the worm is distinctly pathogenic, causing a marked inflammation and erosion of the stomach-wall.

This species is remarkable for the presence, in mature worms of both sexes, of a large, prepuce-like fold of cuticle which more or less completely envelops the caudal end of the body. The lips are rather large and conical, with a large, bluntly conical external tooth and three flattened

* According to the original description by von Linstow the lengths of the spicules were 1.76 mm. and 0.62 mm. Schulz, who has re-examined the type material, gives the length of the left spicule as 3.2 mm., but was unable to see the right spicule.

internal teeth of the same length as the former. The œsophagus is about one-fifth of the total length of the body. The male measures 13 to 40 mm. in length and 0.7 to 1.3 mm. in thickness. The caudal papillæ are arranged as indicated in Fig. 183, *A*. The left spicule is 1 to 1.2 mm. long, the right spicule, which is slightly stouter, 0.84 to 0.9 mm. The female is 15 to 48 mm. long and 1 to 1.7 mm. thick. The vulva is a little in front of the

middle of the body, and the uterus has two branches. The eggs measure about 0.049×0.035 mm.

***Physaloptera gemina* v. Linstow, 1899**, originally recorded from the stomach and intestine of the cat in Egypt, has also been recorded from the fowl by Railliet. The male is 11.4 mm. long and 0.47 mm. thick, the female 19 and 0.53 mm. respectively. Each lip has apparently three apical teeth and a number of internal denticles. The caudal papillæ of the male are arranged as indicated in Fig. 183, *B*. The number of uterine branches is unknown. The eggs measure 0.052×0.032 mm.

***Physaloptera pacitæ* Tubangui, 1925**, is a species recorded from the stomach-wall of the cat in the Philippines. The male is 19 to 22 mm. long, the female 23 to 25 mm. The lips have a large external tooth and three smaller internal teeth. The œsophagus is

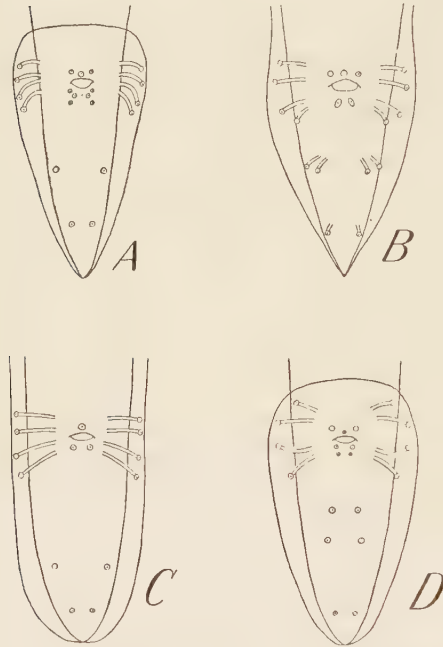


FIG. 183.—DIAGRAMS OF THE POSTERIOR END OF THE MALE (VENTRAL VIEW) IN VARIOUS SPECIES OF *Physaloptera*, SHOWING ARRANGEMENT OF PAPILLÆ. (ORIGINAL.)

(*A*), *P. præputialis*; (*B*), *P. gemina*;
(*C*), *P. pacitæ*; (*D*), *P. truncata*.

4.4 to 4.8 mm. long. The left spicule measures 0.91 mm. in length, the right about 0.68 mm. The arrangement of the caudal papillæ is shown in Fig. 183, *C*. The vulva is at the level of the posterior end of the œsophagus. The eggs measure 0.048 to 0.05×0.03 mm.

***P. rara* Hall and Wigdor, 1918**, is recorded from the duodenum of the dog in Michigan, U.S.A. The male is unknown. The female measures 24 mm. in length and 1.34 mm. in thickness. The lips are partly retractile, and have a rather small external tooth and three prominent internal teeth. The œsophagus is 1.16 mm. long, the tail 0.42 mm. The vulva is situated at 3.63 mm. from the anterior end, and the uterus

has two branches. It has been suggested that this may have been an accidental parasite of the dog.

P. truncata Schneider, 1866, was recorded from the crop of the fowl in Brazil. The length of the male is given as 25 mm., that of the female as 33 mm. The external tooth of each lip is truncate and widened anteriorly, while the three internal teeth are broad and somewhat heart-shaped in outline. The arrangement of the caudal papillæ is indicated in the accompanying diagram (Fig. 183, D).

The subfamily **Thelaziinæ** contains several genera in which the lips are inconspicuous, and cuticular head-shields are absent. There is a buccal capsule, of variable shape, but usually small, and without annular or spiral thickenings in its wall. The males typically possess numerous sessile preanal papillæ and are without an accessory piece. Some of the genera show a marked predilection for situations in or connected with the eyes of their hosts.

In the genus **Thelazia** Bosc, 1819, the transverse striations of the cuticle are usually coarse and prominent, resembling in profile the teeth of a saw. The anterior edge of the buccal capsule is cut into six festoons or indentations. The shape of the capsule is variable. The tail of the male is short and without alæ. The preanal papillæ are generally numerous, and include an unpaired precloacal papilla. There are from two to four pairs of postanal papillæ. The spicules are unequal. The tail of the female is short and blunt. The vulva is in the anterior region, and the uterine branches are parallel and run posteriorly. The worms are viviparous. The favourite situation of the species of this genus is the lachrymal ducts of mammals

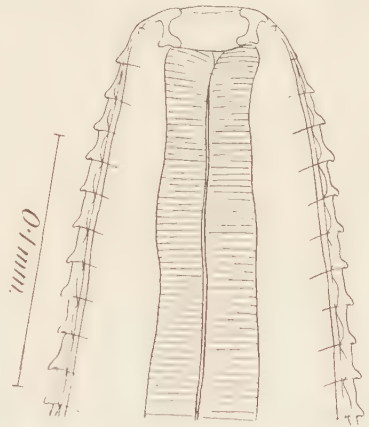


FIG. 184. *Thelazia rhodesii*: ANTERIOR END OF FEMALE, LATERAL VIEW. (ORIGINAL.)

and birds. Not infrequently, however, they wander over the surface of the cornea or beneath the eyelids or nictitating membrane. They may cause a more or less severe conjunctivitis and other symptoms, and occasionally even penetrate into the interior of the eye. Several species occur in domestic animals, more particularly in cattle.

Thelazia rhodesii (Desmarests, 1828) is a fairly common parasite of the ox and buffalo, and has been met with in Europe, Asia (Sumatra,

China) and Africa. In this species the cuticular striations are very coarse and prominent. The male is 8 to 12 mm. long, the female 12 to 18 mm. The buccal capsule is short and wide, being widest in the middle of its length. The œsophagus is 0.54 to 0.6 mm. long. The male has about fourteen pairs of preanal papillæ and three (?) pairs of postanal papillæ. The spicules measure 0.75 to 0.85 and 0.115 to 0.13 mm. respectively in length. The vulva is situated at 0.9 to 1 mm. from the anterior end.

T. gulosa Railliet and Henry, 1910, has been met with in cattle in France and Sumatra. The cuticle is relatively finely striated. The male measures 6 to 9 mm. in length, the female 11 to 14 mm. The buccal capsule is cup-shaped and widest in front. The œsophagus is 0.3 to 0.32 mm. long. The male has about fourteen pairs of preanal and four pairs of postanal papillæ, and the spicules measure 0.99 to 1.025 and 0.12 to 0.125 mm. The vulva is at 0.45 to 0.5 mm. from the anterior end.

A third form, **T. alfortensis** Railliet and Henry, 1910, has been described from the ox in France. This is distinguished from *T. gulosa* chiefly by its cylindrical buccal capsule. The male is unknown. The female measures 7 to 11 mm. in length, and has an œsophagus 0.28 to 0.35 mm. long. The vulva is at 0.4 to 0.5 mm. from the anterior end.

T. lacrymalis (Gurlt, 1831) occurs in the eyes of horses. It is a form measuring 8 to 12 mm. in length in the male, 14 to 18 mm. in the female. The cuticular striations are relatively fine but prominent. The buccal capsule is widest at its base, and measures about 0.01 mm. in length and 0.021 mm. in width. The œsophagus is 0.32 to 0.4 mm. long. The spicules of the male measure respectively 0.17 to 0.19 and 0.13 to 0.14 mm., and there are about ten pairs of preanal and three pairs of postanal papillæ. The vulva is at 0.56 mm. from the anterior end.

T. callipæda Railliet and Henry, 1910, occurs under the nictitating membrane of the dog in India and China. Two recorded cases of the occurrence of *Thelazia* in the human eye in China have recently (1927) been shown by Faust to be attributable to this species. Faust has also described the male worm, which was hitherto unknown. In this species the cuticle is rather finely striated. The buccal capsule is 0.025 mm. long, and is narrow at the base, wider (0.033 to 0.034 mm.) in the anterior third, and narrower again at its opening. The œsophagus is 0.67 mm. long (in the female). The male measures 7 to 11.5 mm. in length, the female 7 to 17 mm. The former has only five pairs of preanal papillæ, in addition to a median papilla in front of the cloaca, and two pairs of postanal papillæ. The left spicule is about twelve times as long as the right, but their actual lengths are not stated by Faust. The vulva is situated at about 0.55 mm. from the anterior end.

A species, *T. leesei* Railliet and Henry, 1910, has been met with several times in camels in India. The length of this form is about 12 mm. in the male, 15 to 21 mm. in the female. The buccal capsule is narrowed gradually in front, but its walls are thickened posteriorly so as to reduce the lumen. The spicules of the male measure 0.34 and 0.105 mm. respectively.

The genus *Oxyspirura* v. Drasche, in Stossich, 1897, contains a number of species which occur under the nictitating membrane of the eyes, or in the orbital and nasal cavities, of birds. In these forms the tail in both sexes is generally tapering, and in the male the caudal end is laterally compressed, without alæ, and generally curved ventrally or spirally coiled. The caudal papillæ are sessile, variable in number and often asymmetrical on the two sides. The spicules are very unequal. The vulva of the female is near the posterior end of the body.

Oxyspirura mansonii (Cobbold, 1879) occurs in the fowl, turkey and peafowl in many parts of the world. It is a form measuring 10 to 16 mm. in length in the male and 12 to 19 mm. in the female. The maximum thickness of the male is 0.2 to 0.35 mm., that of the female 0.4 to 0.43 mm. The œsophagus is about 1.5 mm. long. The tail of the male is 0.32 to 0.4 mm. long, and is curved ventrally. There are four pairs of preanal and two pairs of postanal papillæ. The left spicule is slender and 3 to 3.5 mm. long, the right boat-shaped and 0.2 to 0.22 mm. long. The tail of the female measures 0.4 to 0.53 mm. in length, and the vulva is at 1 to 1.4 mm. from the posterior extremity. The eggs measure 0.05 to 0.065 × 0.04 to 0.045 mm.

O. parvovum Sweet, 1910, is a very similar form* occurring in the fowl in Australia, and recently recorded also from the Muscovy duck (*Cairina moschata*) and (experimentally) from the pigeon in Queensland. The male is 9.2 to 14.5 mm. long and 0.26 to 0.3 mm. thick, the female 13.5 to 20 and 0.27 to 0.39 mm. respectively. The tail of the male is 0.23 to 0.3 mm. long and is sharply curved ventrally. There are three pairs of preanal and two pairs of postanal papillæ. The spicules measure 3.4 to 4.1 and 0.18 to 0.24 mm. respectively. The tail of the female is

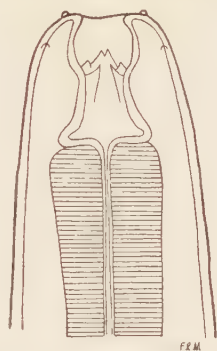


FIG. 185.—*Oxyspirura mansonii*: ANTERIOR END, VENTRAL VIEW. (AFTER YORKE AND MAPLESTONE.)

* The description here given is that of Sweet. In view of a recent account of the Australian worm given by Fielding, however, it seems very probable that *O. parvovum* should be regarded as a synonym of *O. mansonii*.

0.39 to 0.44 mm. long, and the vulva is at 0.78 to 1.07 mm. from the posterior end. The eggs are, according to Sweet, considerably smaller than in *O. mansonii*, measuring only 0.033 to 0.045 $\times$ 0.025 to 0.03 mm.

The eggs of *O. mansonii*, after being washed down the lachrymal canals, are swallowed by the bird and passed with its droppings. It has been found that they are capable of hatching in two or three days in the open, and it therefore seems possible that the intermediate host, if any, may be infected not by swallowing the eggs but by active penetration on the part of the larvæ. By whatever means the worms enter the host, their growth seems to be very rapid, since mature worms have been found in chicks ten days old. Fielding has recently published the results of certain experiments which indicate that in Queensland a cockroach (*Pycnocelus (Leucophæa) surinamensis*) acts as an intermediate host for *O. parvovum*.* The cockroaches apparently become infected by swallowing eggs from droppings or from the ground. These pass through the wall of the alimentary canal of the insect and become encapsuled on its outside. On reaching the infective stage, they may leave their capsules and wander about the interior of the host. In Fielding's opinion the escape of the larvæ from the cockroach takes place in the crop of the bird, whence they pass up the œsophagus to the mouth, and eventually up the naso-lachrymal ducts. In some of the experiments worms appeared in the eyes of chicks or ducklings within a few minutes of their introduction into the mouth.

The relationships of the genus **Rictularia** Frölich, 1802 (= *Laphyctes* Dujardin, 1845; *Pterygodermatites* Wedl, 1861) are very uncertain, but it seems possibly to bear some relation to the Thelaziinæ. The species of this genus are found in the small intestine of mammals (carnivores, bats and rodents). The external appearance is very characteristic, the cuticle being armed along the sides with two subventral series of large, flattened, comb-like spines, at least in the anterior region. Posteriorly the spines become scarcer and diminish in size. The mouth is subterminal, opening dorsally by a transversely elongated aperture bordered by small denticles. There is a small, well-chitinated buccal capsule, armed at its base with teeth and spines. The œsophagus is simple and slightly club-shaped. The caudal end of the male is conical, and may or may not be provided with somewhat bursa-like alæ. Several pairs of preanal and postanal papillæ are present. The spicules are short and equal or subequal, and there is an accessory piece. The vulva of the female is at about the level of the posterior end of the œsophagus. The uterine branches are parallel and run posteriorly. The eggs contain embryos when laid.

* Kobayashi, in Formosa, has also observed the development of *O. mansonii* in the same insect.

Rictularia cahirensis Jägerskiöld, 1904, occurs in the intestine of the cat and dog in Egypt and Turkestan, and has also been recorded from a civet cat in India and from the South American Azara's fox in captivity in England. The male measures 4.8 mm. in length and 0.176 mm. in thickness, the female 10.5 to 13.5 and 0.27 to 0.32 mm. respectively. The male has about ninety-six pairs of "combs," which extend to the posterior end, and also seven median, ventral combs in front of the cloaca. In the female there are forty-six to fifty-two pairs of prevulvar "combs" and seventy-eight to eighty-four pairs of postvulvar "combs" and spines. The œsophagus measures 1.36 mm. in length in the male, 2.24 to 2.262 mm. in the female. The tail of the male is 0.14 mm. long, and the spicules 0.17 mm. In the female the tail measures 0.16 to 0.208 mm. in length, and the vulva is situated at 2.26 to 3.04 mm. from the anterior end. The eggs measure 0.039 to 0.042×0.026 to 0.028 mm.



FIG. 186.—*Rictularia cahirensis*: ANTERIOR END, LATERAL VIEW. (AFTER JÄGERSKIÖLD, MODIFIED.)

GNATHOSTOMIDÆ.

In the family **Gnathostomidæ** the lips are large and trilobed, each having the cuticle of its inner surface thickened and usually raised into longitudinal tooth-like ridges which meet or interlock with those of the other lip. The female has two or four uterine branches, and the eggs have thin shells, ornamented with fine granulations or dimples.

The subfamily **Gnathostominæ** contains three genera characterized by the presence, behind the lips, of a cuticular "head-bulb" provided either with prominent transverse striations or with transverse rows of backwardly-directed hooks, and containing four membranous submedian "ballonets," the cavity of each of which is in communication with one of four elongated, blind "cervical sacs." The latter are apparently contractile, and serve for the compression of a contained fluid, thus expanding the "ballonets" and making the head-bulb a very efficient "holdfast" when it is buried in the host's tissues.

In **Gnathostoma** Owen, 1836 (= *Cheiracanthus* Diesing, 1838) the head-bulb is armed with simple hooks, and the body with backwardly-

directed cuticular spines. The latter are flattened and scale-like in the anterior region, with their free posterior edges denticulate. Posteriorly they become gradually less subdivided until finally they appear as simple spines or disappear altogether. The male has four pairs of large lateral caudal papillæ with swollen peduncles, and two or more pairs of smaller, sessile, ventral papillæ. The spicules are unequal. The vulva of the female is usually behind the middle of the body. The vagina is long, and there are two uterine branches. The members of this genus occur as adults in carnivorous mammals, their usual habitat being the wall of the stomach.

Gnathostoma spinigerum Owen, 1836 (= *Cheiracanthus robustus* Diesing, 1838; *C. siamensis* Levinsen, 1889) occurs in the stomach of the cat, dog and various wild Carnivora such as the tiger and leopard. It has been recorded from various parts of the world, including India, China,

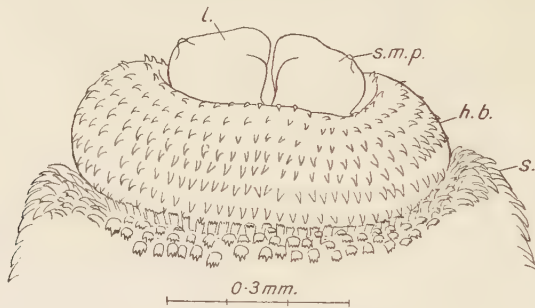


FIG. 187.—*Gnathostoma spinigerum* : ANTERIOR END, DORSAL VIEW.
(AFTER BAYLIS AND LANE, IN *Proc. Zool. Soc.*)

h.b., head-bulb; *L.*, lip; *s.*, spines of body; *s.m.p.*, submedian papilla.

Siam, North and South America and the Philippines. A few cases of its accidental occurrence in man have been recorded, the worms being found as "erratic" parasites in the subcutaneous tissue, where they sometimes cause the formation of tumours. In its normal hosts this worm burrows in the stomach-wall, where it causes the formation of hard, thick-walled tumours. These not infrequently acquire an opening into the abdominal cavity, and the death of the host from peritonitis may result. Each tumour may contain from one to nine worms. Chandler, from his observations on domestic cats in Calcutta, believes that the incidence of *Gnathostoma* is seasonal, and that it is "consistently lethal" to its hosts. Fully-formed gastric tumours were only found between August and November, while from January to April only immature worms, as a rule, occurred. These were generally found burrowing in the liver, peritoneum, mesentery or diaphragm. "I do not hesitate," Chandler says, "to

consider *G. spinigerum* by all odds the most deadly parasite to which the cat is subject. In fact I know of no other parasite in the whole realm of helminths which can be as consistently injurious to its host in a short period of time."

G. spinigerum measures 10 to 25 mm. in length in the male, 9 to 31 mm. in the female. Its maximum thickness, in the male, is 1 to 1.9 mm., in the female 1 to 2.5 mm. The head-bulb has a transverse diameter of about 0.52 to 0.6 mm., and bears from six to eleven rows of hooks. The spines cover about the anterior two-thirds of the body. The maximum number of denticulations on the most anterior spines is from three to four. The ventral surface of the caudal end of the male, except for a Y-shaped area surrounding the cloaca, is also covered with transverse rows of small spines. The left spicule of the male measures 1.1 to 2.63 mm. in length, the right spicule 0.4 to 0.8 mm. The vulva

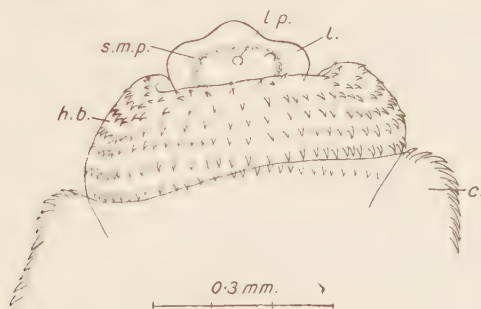


FIG. 188.—*Gnathostoma spinigerum*: ANTERIOR END, LATERAL VIEW.
(AFTER BAYLIS AND LANE, IN *Proc. Zool. Soc.*)

c., "collar"; h.b., head-bulb; l., lip; l.p., lateral papilla; s.m.p., submedian papilla.

of the female is at 4 to 8 mm. from the posterior end. The eggs measure about 0.06×0.035 mm. and have a thin cap at one pole.

The life-history of *Gnathostoma* is not yet understood. In addition to the immature forms found in the final hosts of *G. spinigerum*, Chandler has observed larvæ of *Gnathostoma* encapsuled in the mesentery of snakes (pythons and cobras), while others have been recorded from birds (eagle and pelican). It is not certain, however, to what species these larvæ belong. Their connection with the adult of *G. spinigerum* or any other known species has not been definitely established. The larvæ of one of the species of the closely-related genus *Echinocephalus* are known to occur in the pearl-oyster and another marine bivalve mollusc (*Pinna*), while the adults occur in Elasmobranch fishes which feed upon these shellfish. It is possible, therefore, that the first larval host of *Gnathostoma* may likewise be a mollusc, or at least some invertebrate.

Gnathostoma hispidum Fedchenko, 1872, occurs in the stomach of the pig and wild boar in Eastern Europe and Asia. It has once been recorded doubtfully from the ox, while it appears, like *G. spinigerum*, to occur as an occasional, "erratic" parasite in man in China and Japan, its habit of tunnelling in the subcutaneous connective tissue being among the causes of the so-called "creeping disease."

This species measures 15 to 25 mm. in length and 1.18 to 2 mm. in thickness in the male; 22 to 45 and 1.78 to 2.5 mm. respectively in the female. The head-bulb has a transverse diameter of about 0.75 mm., and bears nine to twelve rows of hooks. The entire body is covered with spines, the most anterior of which have seven to nine denticulations. More posteriorly they have three points, the middle point being the longest, while in the hinder half of the body they are simple and hair-like. In the fresh condition the anterior portion of the body is blood-red, the posterior portion grey, streaked with yellowish. The left spicule of the male is 0.88 to 1.29 mm. long, the right spicule 0.32 to 0.4 mm. The vulva of the female is situated in the middle region of the body, but its position is apparently variable. The eggs measure about 0.072 to 0.074 $\times$ 0.039 to 0.042 mm., and have a wart-like cap at one pole.

This parasite buries itself deeply in the gastric mucosa, causing the formation of a cavity containing blood-stained fluid and surrounded by a reddened area. When numerous, the worms may give rise to a chronic gastritis. Immature forms are also found wandering in the liver and veins, and may set up a thickening of the interlobular connective tissue of the former organ.

Gnathostoma doloresi Tubangui, 1925, is a form recorded from the stomach of the pig in the Philippines. The male is unknown. The female measures 30 to 41 mm. in length and 3.14 to 3.37 mm. in maximum thickness. The anterior third of the body is much thinner than the posterior two-thirds. The width of the head-bulb is 0.74 to 0.85 mm., and it bears ten rows of hooks. The body is entirely covered with spines, the most anterior of which have six or seven points. At about 9 to 11 mm. from the anterior end the spines become simple. The vulva is behind the middle of the body. The eggs measure 0.06 to 0.063 $\times$ 0.037 mm., and are said to differ from those of *G. hispidum* in having a wart-like process at *each* pole.

THE ORDER DIOCTOPHYMOIDEA.

DIOCTOPHYMIDÆ.

In the family **Dioctophymidæ** are placed the peculiar genera *Dioctophyme* Collet-Meygret, 1802, *Eustrongylides* Jägerskiöld, 1909, and *Hystrichis* Dujardin, 1845. These have the following characters in common:

Each of the four muscular fields divided longitudinally into two by the insertion of highly developed suspensory muscles connecting the alimentary canal with the body-wall. Mouth hexagonal, surrounded by one, two or three crowns each of six papillæ. Œsophagus relatively long, simple or club-shaped. Tail of male furnished with a terminal bursa-like expansion, without rays. A single spicule present. Anus of female terminal. Female genital tube single. Eggs barrel-shaped, with a thick, pitted, albuminous coating and not containing embryos when laid.

Dioctophyme renalis (Goeze, 1782) (= *Eustrongylus gigas* (Rudolphi, 1802) of many authors), the only known species of its genus, is the largest Nematode known. It is a parasite of the kidneys and peritoneal cavity

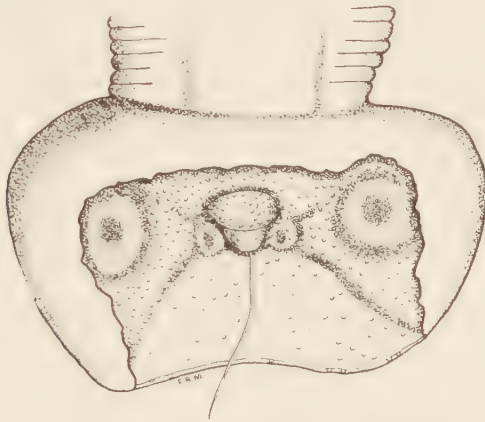


FIG. 189.—*Dioctophyme renalis* : POSTERIOR END OF MALE, VENTRAL VIEW. (AFTER STEFANSKI.)

of the dog, and has been recorded as an occasional parasite of the pig, horse, ox and man. It occurs also in certain wild carnivores, including the wolf, otter, seal and various members of the weasel tribe. Its usual habitat is the pelvis of the kidney, from which it may invade the body of the organ and gradually destroy the renal tissue. Individuals are also met with either free or encapsuled in the abdominal cavity (especially between the lobes of the liver), in the liver itself, and (more rarely) in the thoracic cavity.

The body of this worm is blood-red when fresh. The female measures from 200 mm. to about 1 metre in length and 5 to 12 mm. in thickness. The male is little more than one-third of this size (140 to 450 mm. long and 3 to 4 mm. thick). Each lateral line bears a row of papillæ, which become closer together towards the extremities of the body. The mouth

is surrounded by two crowns of papillæ, those of the posterior crown being situated on relatively large nodular swellings, while those of the anterior crown are small and simple. On the ventral side, behind the mouth, there is a short, longitudinal depression with rather prominent borders. The "bursa" of the male is oval and transversely elongate, slightly indented on its anterior margin, and covered on its inner surface with small papilliform elevations. In the centre of the "bursa" is a somewhat elevated cone at the summit of which is the cloacal aperture. The spicule is bristle-like and 5 to 6 mm. long.

The anus of the female is crescentic, and in its neighbourhood there are some small papillæ. The vulva is situated towards the anterior end of the body, but behind the œsophageal region. In females of different sizes its position varies between 14 and 75 mm. from the anterior end. The eggs have a coarsely pitted albuminous coating when laid, and measure about 0.064×0.044 mm.

This parasite sometimes induces nervous symptoms in dogs which simulate those of rabies. Its life-history has not yet been fully elucidated. Ciurea, however, has recorded the occurrence of larval forms which he believes to belong to it in a European fresh-water fish, *Idus idus*. A dog which had been fed on fourteen of these fish was found, on post-mortem examination some five months later, to contain an adult worm. Encapsuled larval forms of the closely-related genus *Eustrongylides* are not uncommon in fresh-water fishes, and it appears highly probable that fishes do act as intermediate hosts for *Diectophyme*. This would readily explain the infection of fish-eating animals, such as otters and seals, with the adult, though it is less easy to account for the infection of some of the other hosts.

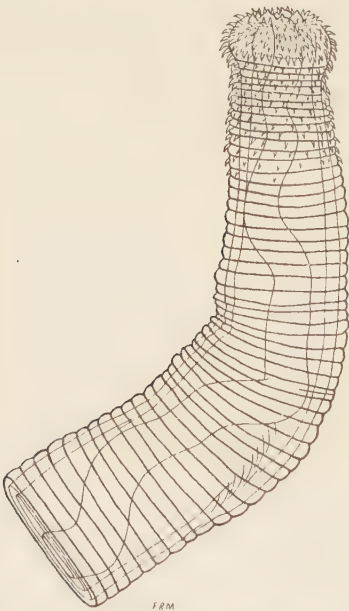


FIG. 190.—*Hystrichis tricolor*: ANTERIOR END OF FEMALE. (AFTER JÄGERSKIÖLD, MODIFIED.)

The adult forms of *Eustrongylides* and *Hystrichis* occur in fish-eating, or at least more or less aquatic, birds.

The former genus is not known to occur in domesticated birds, but two species of *Hystrichis* have been so recorded.

In this genus the "head" is usually more or less swollen and sometimes subglobular. The body is cylindrical, or sometimes swollen in its

middle portion. The cuticle is coarsely striated towards the extremities and bears transverse rows of spines, which may be confined to the anterior region, or to the swollen "head." The mouth is surrounded by a single crown of papillæ. The vulva of the female is situated posteriorly, close to the anus.

Hystrichis tricolor Dujardin, 1845, occurs in the glands of the proventriculus of the domestic duck and various wild ducks in Europe. The name of the species has reference to the fact that, while the cuticle is whitish, the body is partly coloured red, presumably by ingested blood, and the intestine appears blackish. The male measures about 25 mm. in length, the female 27 to 40 mm. The anterior end of the body bears forty to forty-two transverse rows of spines. The eggs measure 0.085 to 0.088 × 0.036 to 0.04 mm.

H. cygni (Molin, 1858) (= *pachicephalus* Molin, 1861) is a little-known form recorded from the swan in Italy, and said to occur between the external coats of the ventriculus. The male is unknown. The female is 30 mm. long, and the body shows irregular swellings. At the anterior end there is a bulbous expansion which is wider than long and bears twenty rows of large spines. There are also spines on the body itself anteriorly.

THE ORDER TRICHINELLOIDEA.

In this group the body is more or less clearly divided into an anterior, or œsophageal, portion and a posterior portion containing the intestine and the genital organs. Frequently the œsophageal portion is of narrower calibre than the posterior portion. The œsophagus is remarkable in the fact that it is entirely non-muscular, and consists of a narrow cuticular tube embedded in a single chain of cells arranged in "drain-pipe" fashion. The anus is terminal or subterminal in both sexes. The male has a single spicule or none. When present, the spicule is contained in a protrusible membranous sheath. The vulva is situated at or near the junction of the œsophageal and posterior portions of the body. In all cases the female genital tube is single.

TRICHINELLIDÆ.

The order contains the single family **Trichinellidæ**, which may be divided into three subfamilies. The subfamily **Trichosomoidinæ** contains only one genus and species, *Trichosomoides crassicauda*, a parasite of the bladder of rats, and peculiar for the habit of the male of living like a parasite in the vagina or uterus of the female. The subfamily **Trichinellinæ** likewise contains a single genus, **Trichinella** Railliet, 1895 (= *Trichina* Owen, 1835, preoccupied). This is represented by the interesting

species *Trichinella spiralis* (Owen, 1835), one of the most dreaded of human parasites, but one which is fortunately now much less common than it was in the past, before its importance was fully understood.

The adult forms of *T. spiralis* occur in the small intestine of their hosts, which include a large number of mammals besides man. It is probable, indeed, that almost all kinds of mammals are susceptible to

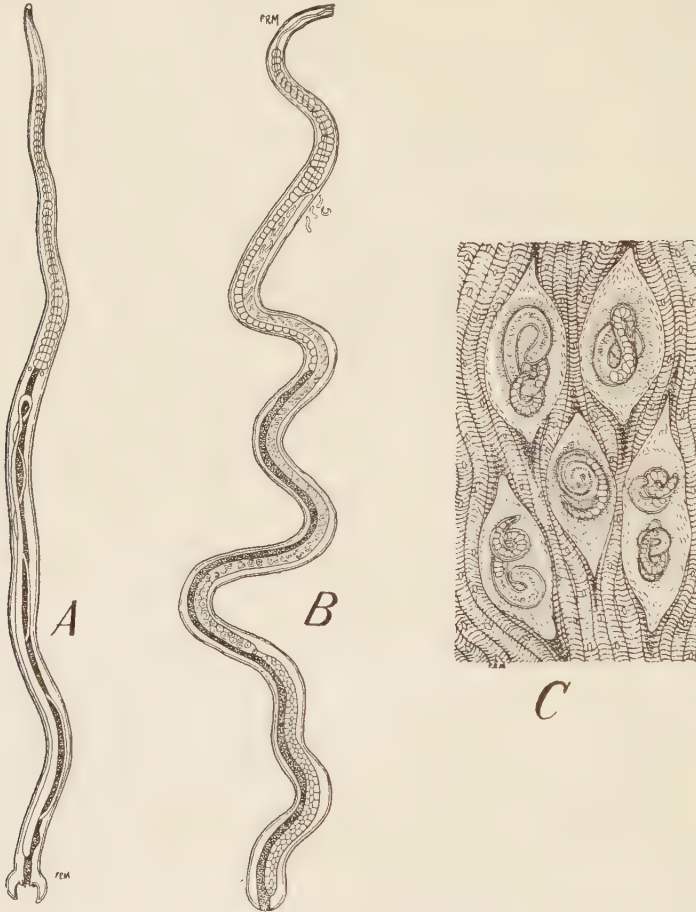


FIG. 191.—*Trichinella spiralis*. (AFTER FIEBIGER.)

A, adult male; B, adult female; C, larvæ encapsuled in muscle.

infection with this worm. Among domestic animals it has been recorded, at least experimentally, in the pig, ox, sheep, horse, dog and cat. It also occurs naturally in rabbits, rats and many other rodents, and in a number of other wild mammals. The pig and the rat are probably its chief hosts. It is a parasite of world-wide distribution, and was formerly very common (and still occurs sporadically) in human beings in countries where pork

is consumed in a raw or very slightly cooked state. Improved methods of meat inspection have, however, materially reduced its incidence.

The male worm is 1.4 to 1.6 mm. long and about 0.04 mm. thick. The posterior end has a pair of large, ventrally-directed processes at the sides of the cloaca, and between these two pairs of papillæ. There is no spicule or spicule-sheath. The female measures 3 to 4 mm. in length and 0.06 mm. in thickness. The vulva is situated near the middle of the œsophageal region, at about one-fifth of the total length of the body from the anterior end. The worm is ovoviviparous, the subspherical eggs, which measure 0.01 to 0.03 mm., having a thin membrane but no true shell. The embryos, on escaping from them, measure 0.09 to 0.16 mm. in length and 0.006 to 0.009 mm. in thickness, the greatest thickness being near the anterior end.

The life-history of this worm is of peculiar interest. After copulation, which takes place in the small intestine of the host, the male dies. The fertilized female burrows into the mucosa by way of the glands of Lieberkühn, and makes its way into the lymph-spaces. Here it produces a large number of embryos, which migrate by way of the lymphatics and blood-vessels all over the body, until they reach the connective tissue of the voluntary muscles, especially those of the diaphragm, chest-wall, tongue, throat and eye. They now penetrate into the sarcolemma of the muscle-fibres, and grow to a size of 0.8 to 1 x 0.03 mm., their shape changing at the same time so that the anterior end becomes slender, the posterior end thick and blunt. Finally they become encapsuled in this situation in lemon-shaped capsules, each of which usually contains a single larva, but sometimes as many as seven. If not ingested by a suitable host, the larvæ ultimately die, and the capsules undergo fatty degeneration and finally become calcified. The encapsuled larvæ may, however, remain alive and infective for as long as eleven years in the pig's muscles, while cases have been recorded where larvæ were believed to have lived for twenty-one or twenty-four years in man.

When ingested by another host, the larva is liberated by digestion from the capsule within twenty-four hours, undergoes a final moult, and becomes sexually mature in the intestine within one to five days. On first being ingested, the larvæ may set up an intense form of diarrhœa if present in large numbers. The worms appear also to produce a definite toxin, the serum of infested animals having a toxic effect when injected into other animals. The muscles invaded by the larvæ may undergo degeneration and become painful or immovable. In severe cases death may occur from paralysis of the respiratory muscles.

The salting of pork is not always sufficient of itself to kill the contained larvæ, though some methods of curing appear to be effective. The larvæ

are, however, readily killed by heat, while Ransom has shown that cold storage at -15°C. ($=5^{\circ}\text{F.}$) for at least twenty days kills most of them.

In the subfamily **Trichurinæ** the male possesses a spicule or, exceptionally, only a spicule-sheath. The eggs are lemon-shaped, having a thick shell with an aperture at each pole closed by a prominent plug. Their contents are unsegmented at the time of laying. The development, where known, is direct.

In the genus **Trichuris** Roederer, 1761 ($=$ *Trichocephalos* Goeze, 1782; *Trichocephalus* Schrank, 1788) the œsophageal portion of the body is very slender, and longer than the posterior portion, which is usually much stouter (hence the name "whipworm," often applied to members of the genus). The posterior extremity is blunt and rounded in both sexes. On the ventral surface of the œsophageal portion there is a longitudinal "bacillary band," composed of numerous rod-like unicellular subcuticular glands. The caudal end of the male is curled dorsally. The spicule is



FIG. 192.—*Trichuris trichiura*. (FROM CASTELLANI AND CHALMERS, AFTER CLAUS.)

Male on right, female on left.

contained in a protrusible, prepuce-like sheath, of which the inner surface (which becomes the outer surface in the evaginated condition) may be smooth or spiny. The vulva is just behind the junction of the two portions of the body. The egg-shells are usually of a dark brown colour. The species of this genus occur in the large intestine (especially the cæcum) of mammals, where the worms bury their anterior ends in sinuous burrows in the epithelium. Several species occur in domestic animals, and one of these also in man.

Trichuris trichiura (Linnæus, 1771) ($=$ *Trichocephalus hominis* Schrank, 1788; *T. suis* Schrank, 1788; *T. apri* Gmelin, 1790; *T. dispar* Rudolphi, 1802; *T. crenatus* Rud., 1809) occurs in man, in various other primates and in the pig. It inhabits the cæcum, colon and appendix, and is of cosmopolitan distribution.

The male is 30 to 45 mm. in length, the female 35 to 50 mm., and the œsophageal portion occupies about two-thirds of the total length.

The spicule of the male is 2 to 3.35 mm. long, and has a rounded or pointed tip. The spicule-sheath is variable in shape when extruded, being sometimes cylindrical, sometimes expanded, and may be partly or wholly covered with spines. The eggs measure 0.05 to 0.056 × 0.021 to 0.025 mm. Their contents are unsegmented when laid. The development of the embryos cannot take place within the body of the host, but only in the open. Segmentation is usually slow in temperate countries, where the development to the infective stage may take six to twelve months. In warm climates, or under experimental conditions with a

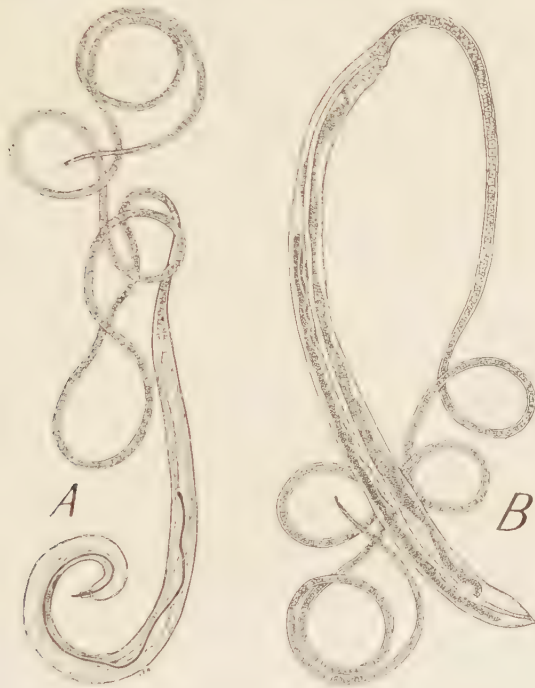


FIG. 193.—*Trichuris vulpis*. (AFTER FIEBIGER.)

A, male; B, female.

constant high temperature, it is more rapid, three weeks to a month being required. The eggs are very resistant to cold, and can withstand freezing, while the infective embryos remain viable for a long period, Davaine having observed them to live for five years. Upon the eggs being ingested (with contaminated food or water) by a suitable host, the larvæ hatch and are said to pass at once into the mucosa of the intestine, without migration. In the closely-allied species *T. vulpis*, however, according to Neshi, they migrate through the wall of the stomach and by way of the blood-stream and lungs, like those of *Ascaris* and the hookworms. The

worms develop rapidly to maturity, and begin to lay eggs less than a month after infection.

Trichuris vulpis (Frölich, 1789) (= *Trichocephalus depressiusculus* Rudolphi, 1809) occurs in the cæcum of the dog and fox. It is a species measuring 45 to 75 mm. in length, of which the œsophageal region occupies about three-quarters. The spicule of the male is 9 to 11 mm. long. The spicule-sheath is covered with blunt spines in the region nearest to the cloaca, but smooth elsewhere. The eggs measure 0.07 to 0.08 × 0.037 to 0.04 mm.

Two species of *Trichuris* have been recorded from the cat in South America. These are **T. serrata** (v. Linstow, 1879) and **T. campanula** (v. Linstow, 1889). According to Urioste, who has examined material from cats in Brazil, the latter is a synonym of the former. There is, however, a considerable difference between the measurements of *T. serrata* as given by von Linstow and by Urioste, and the latter's agree very closely with the original description of *T. campanula*.

In *T. serrata*, according to von Linstow, the male is 40 mm. long, the female 48 mm. The anterior portion of the body is about two-thirds of the total length. The spicule of the male is 3.9 mm. long, and its sheath is covered with conical spines throughout, the spines becoming smaller towards the end. The vulva has a protruded vagina, which is also said to be spiny. The eggs measure 0.056 × 0.039 mm.

As regards *T. campanula*, von Linstow states that the œsophageal region is four-fifths of the total length (in the female). The length of the male is not given, but that of the female is 31.5 mm. Urioste, describing what he regards as *T. serrata*, gives the

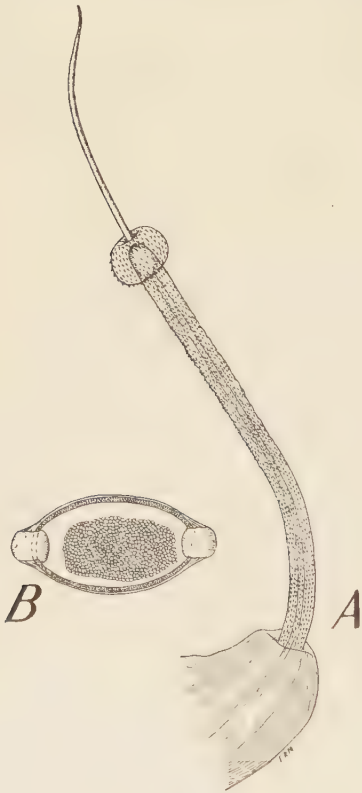


FIG. 194.—*Trichuris ovis*.
(AFTER RANSOM.)

A, posterior end of male, with extruded spicule and sheath; B, egg.

length of the male as 20.5 mm., that of the female as 23 mm., the length of the spicule as 1.5 mm., and the dimensions of the eggs as 0.08 × 0.036 mm.

Several species of this genus have been described from domestic and other ruminants. Of these the best known is the common and widely distributed *Trichuris ovis* (Abildgaard, 1795) (*Trichocephalus affinis* Rudolphi, 1802). This species occurs in the large intestine of the sheep, goat, ox, camel, llama and numerous wild ruminants. Both sexes are about 50 to 80 mm. long. In the male the œsophageal portion is about three-quarters, in the female two-thirds to four-fifths of the total length. The marginal rods of the bacillary band are larger than the rest. The spicule of the male is 5 to 6 mm. or more in length, and ends in a sharp point. The spicule-sheath is very long, covered with small spines and expanded distally, when evaginated, into a bulbous swelling. The eggs measure 0.07 to 0.08 mm. in length, including the polar plugs, or 0.055 to 0.065 mm. excluding them, and 0.03 to 0.042 mm. in width.

The chief characters of the other species of interest here may be tabulated as follows:

TABLE XL.—OTHER SPECIES OF *TRICHURIS* IN DOMESTIC RUMINANTS.

Species.	Hosts.	Length in Mm.		Æsophageal Region (Fraction of Total Length).		Spicule (Length in Mm.).	Character of Spicule-sheath.	Dimensions of Eggs in Mm.
		♂	♀	♂	♀			
<i>Trichuris discolor</i> (v. Zeb u, o x Linst., 1906)	(Ceylon, Europe)	45 to 59	43 to 52	About $\frac{2}{3}$	About $\frac{3}{4}$	1.76 to 2.3	Spiny	0.06 to 0.073 × 0.03 to 0.035
<i>T. globulosa</i> (v. Linst., 1901)	Camel, <i>terrus</i> <i>eldi</i>	40 to 70	42 to 60	About $\frac{2}{3}$	About $\frac{3}{4}$	4.2 to 4.8	Spiny, with large globular swelling distally. Spines on swelling larger than elsewhere	0.068 × 0.036
<i>T. cameli</i> (Rudolphi, 1819) (= ? <i>Tricho-</i> <i>cephalus echino-</i> <i>phyllus</i> Nitzsch, in Crepl., 1849) (probably = <i>globu-</i> <i>losa</i>)	C a m e l s (Arabian and Bactrian)	—	—	About $\frac{3}{4}$	—	—	Spiny, with button-like distal enlargement	—
<i>T. skrjabini</i> Baskakov, 1924 (possibly = <i>discolor</i>)	C a m e l s (Arabian and Bactrian)	36	48	$\frac{2}{3}$	$\frac{3}{4}$	0.998	Spiny	0.072 × 0.033

The genus *Capillaria* Zeder, 1800 (= *Trichosoma* Rudolphi, 1819) consists of very slender, hair-like worms closely related to *Trichuris*, but in which the œsophageal portion of the body is usually shorter than the posterior portion, and the latter is not conspicuously thickened. A

ventral "bacillary band" is present, and usually also a similar band dorsally. The single spicule of the male is usually relatively long, and is contained in a protrusible sheath, as in *Trichuris*, the outer surface of which, when evaginated, may be smooth or covered with minute spines. The caudal end of the male is usually provided with a pair of small lobes, which may support a slight membranous bursa-like structure. The cuticle of the body, for a short distance in front of the cloaca, which is subterminal, may be expanded laterally to form slight alæ. The tail of the female is usually blunt, and the anus subterminal. The vulva is situated just behind the œsophageal region, and its lips are sometimes

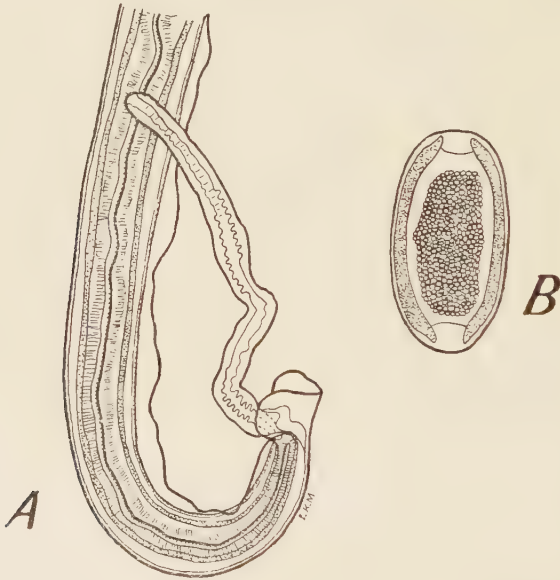


FIG. 195.—*Capillaria brevipes*. (AFTER RANSOM.)
A, posterior end of male, with extruded spicule-sheath; B, egg.

prolonged as a tubular, membranous appendage. The eggs are of the same type as in *Trichuris*, with polar plugs, but are usually colourless.

This genus contains a very large number of species, which occur in the alimentary canal, or occasionally in the urinary bladder, of all groups of vertebrates. Partly on account of their small size and the lack of obvious and striking specific differences, many of these forms have been very briefly described, and the determination of species is often a matter of considerable difficulty.

Two species occur in the small intestine of the sheep, both having been first described by Ransom in the United States. **Capillaria brevipes** Ransom, 1911, is a form measuring 8 to 9 mm. in length in the male and

about 12 mm. in the female, with a maximum thickness of 0.05 to 0.06 mm. The œsophagus is about 4 mm. long in the male, 5 mm. in the female. The spicule of the male is about 0.9 mm. long. The spicule-sheath is considerably longer than the spicule, and is without spines. There are narrow caudal alæ in the male, and a small bursa-like structure supported by a pair of processes whose distal ends are slender and bent forward almost at right angles. The eggs measure 0.05 × 0.025 mm., and have shells 0.003 to 0.004 mm. thick.

C. longipes Ransom, 1911, which occurs in the sheep and also in the North American prong-horned antelope, measures 11 to 13 mm. in length and 0.05 to 0.06 mm. in thickness in the male, and about 20 and 0.08 mm. respectively in the female. The œsophagus of the male is 4 to 5 mm. long, that of the female 6 to 7 mm. The male has rather broad caudal alæ, and the pair of processes supporting the terminal bursa-like membrane have slender distal portions bent forward, as in *C. brevipes*, nearly at right angles. The spicule is about 1.2 mm. long, and its sheath is without spines. The eggs measure 0.045 to 0.05 × 0.022 to 0.025 mm., and have shells only 0.0015 to 0.002 mm. thick.

Capillaria bovis Schnyder, 1906, is a little-known form found in the small intestine of the ox in Switzerland. The male is about 12 mm. long and 0.075 mm. thick, the female measuring about 20 and 0.095 mm. respectively. The eggs measure 0.047 × 0.027 mm.

C. linearis (Leidy, 1856) is a small species recorded from the small intestine of the cat in North America. The male is 3.8 mm. long and 0.21 mm. in maximum thickness, the female 7.6 mm. long and 0.35 mm. thick. The caudal end, in both sexes, is spirally coiled. In the male the cloaca is situated at some distance from the posterior end, and the tail is conical and pointed. In the female the tail is blunt, and has two conical ventral processes at the tip.

A species found by Bellingham in the bladder of a wild cat in Ireland was named **Capillaria felis-cati** by Diesing in 1851. Up to that time no description of it had been given. Wedl, in 1855, recorded the occurrence of what he presumed to be the same species in the bladder of a domestic cat in Egypt. He stated that the female measured 14 to 16 mm. in length, and gave the size of the eggs as 0.061 × 0.032 mm. The species has recently been recorded in Russia.

Capillaria plica (Rudolphi, 1819), a species occurring in the bladder of the fox and wolf, has also been recorded from the dog. The male is 13 to 30 mm. long, the female 30 to 60 mm. The caudal end of the male is obliquely truncate, and provided with a bursa-like membrane which is produced into a point posteriorly. The spicule is blunt, and its sheath appears punctate owing to the crossing of transverse and longitudinal

TABLE XII.—SPECIES OF *CAPILLARIA* PARASITIC IN DOMESTIC BIRDS.

Species.	Hosts.	Habitat.	Length in Mm.		Esophageal Region (Fraction of Total Length).		Width of Bacillary Bands.	Character of Spicule-Sheath.	Dimensions of Eggs in Mm.	Other Features.
			♂	♀	♂	♀				
<i>Capillaria retusa</i> (Rudolphi, 1893)	Fowl, guinea-fowl	Cæca	9.5 to 13	13 to 19	$\frac{1}{3}$ to $\frac{1}{2}$	$\frac{1}{2}$ to $\frac{3}{4}$	Ventral band Spiny about $\frac{1}{2}$ diameter of body	—	0.05 to 0.063 × 0.028 to 0.035	—
<i>C. longicollis</i> (Rudolphi, 1819)	Fowl, pheasant, etc.	Duodenum	20 to 25	40	About $\frac{1}{3}$	—	—	—	—	—
<i>C. annulata</i> (Molin, 1858) (= <i>Trichostrongylus</i> Reibisch, 1893)	Turkey, fowl, pheasant, etc.	Esophagus and crop, in epithelium	15 to 25	37 to 80	$\frac{1}{4}$ to $\frac{1}{2}$	$\frac{1}{2}$ to $\frac{3}{4}$	Ventral band Spiny about $\frac{3}{4}$, dorsal band about $\frac{3}{4}$ diameter of body	Transversely striated	0.06 to 0.065 × 0.025 to 0.028	Cuticle of head inflated, especially in female.
<i>C. caudinflata</i> (Molin, 1858)	Fowl, pheasant, etc.	Small intestine	17	25	—	—	—	—	—	Caudal end of male with large cuticular vesicle.
<i>C. gallina</i> (Kowalevsky, 1895)	Fowl	Large intestine	16.5	34	$\frac{1}{4}$	$\frac{1}{2}$	About $\frac{1}{3}$ diameter of body	—	0.048 to 0.053 × 0.022 to 0.023	Caudal end of male with large "bursa" supported by a pair of L-shaped processes.
<i>C. dubia</i> (Kowalevsky, 1895)	Fowl	Cæca	10.5	14	$\frac{1}{6}$	$\frac{3}{8}$	$\frac{1}{2}$ diameter of body	Spiny	0.047 to 0.052 × 0.023 to 0.027	"Bursa" of male small, but with L-shaped processes as in <i>C. gallina</i> . An annular constriction near anterior end.
<i>C. collaris</i> (v. Linstow, 1873)	Fowl	Intestine	9	9.5	Nearly $\frac{2}{3}$	$\frac{3}{4}$	Nearly $\frac{1}{2}$ diameter of body	With fine bristles	—	—
<i>C. melagris-gallopavoni</i> (Bartle, 1912)	Turkey	Small intestine	12 to 14	24 to 25	$\frac{1}{3}$	$\frac{1}{2}$	—	Spiny, also with longitudinal and transverse striations	—	Cuticle of body apparently spiny, especially on the sides. Male with lateral caudal ala.
<i>C. anatis</i> (Schrank, 1790)	Geese, various wild ducks	Cæca	11 to 13	21 to 28	—	—	About $\frac{1}{3}$ diameter of body	Smooth	—	—
<i>C. contoura</i> (Creplin, 1839)	Duck, many wild birds	Esophagus (free or in epithelium)	12 to 17	27 to 38	Nearly $\frac{1}{3}$	$\frac{1}{2}$	Ventral band Spiny about $\frac{3}{4}$, dorsal band $\frac{3}{4}$ diameter of body	—	0.048 to 0.056 × 0.021 to 0.024	Body spirally coiled.
<i>C. columba</i> (Rudolphi, 1819)	Pigeon, turkey	Fowl, Intestine	8.4 to 11.7	13 to 18	Nearly $\frac{2}{3}$	$\frac{3}{4}$	About $\frac{1}{4}$ to $\frac{1}{3}$ diameter of body	Transversely striated anteriorly	0.044 × 0.023 (Irwin-Smith) 0.05 to 0.062 × 0.02 to 0.027 (Graybill)	Caudal lobes of male connected by a bursa-like membrane.

folds. The vulva has a tubular appendage. The eggs measure 0.06×0.03 mm.

Several species of *Capillaria* occur in domestic birds. Adequate descriptions of most of them, unfortunately, are not available, but their chief characters may be briefly given in the form of a table. Some of these species appear to be of considerable economic importance. Railliet and Lucet have described a fatal form of inflammation of the œsophagus in ducklings, resulting from infection with *C. contorta*, while *C. columbæ* appears occasionally to cause epidemics of enteritis, which may be fatal, among pigeons.

The genus *Hepaticola* Hall, 1916, differs from *Capillaria* chiefly or solely in the absence of a spicule in the male. A membranous spicule-sheath is present. According to Hall, a bacillary band is apparently absent.

Hepaticola hepatica (Bancroft, 1893) is a form occurring in the liver of rats, recorded also doubtfully in the hare and dog, and once recorded from the liver of man in India. The worm itself is rarely seen, but the masses of eggs left by it in the liver tissue, and appearing as yellowish spots, sometimes accompanied by local cirrhosis and partial atrophy of the liver, are not uncommon in rats. The length of the adult worms has been variously given as 4 to 5 or 10 to 12 cm., the female attaining a thickness of 0.1 to 0.12 mm. The œsophageal region is about half the total length in the male, and one-third in the female. The tail of the female is very short, blunt and conical.

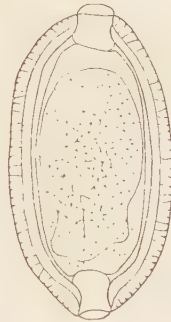


FIG. 196.—*Hepaticola hepatica*:
EGG. (AFTER BAYLIS.)

The vulva is prominent and has a swollen, membranous border, and is situated at 6 to 7 mm. from the anterior end. The eggs, which are provided with polar plugs, measure, according to the writer's observations, 0.0625 to 0.0675×0.03 to 0.0325 mm. Their dimensions have been variously given by other authors as from 0.04 to 0.055 mm. in length and from 0.028 to 0.035 mm. in width. The outer layer of the shell is traversed by numerous minute rod-like structures, ending at the surface in refringent knobs or points, and giving it the appearance, in optical section, of being radially striated.

The life-history of this worm is direct, the infective eggs, if swallowed by a suitable host, hatching in the alimentary canal (especially the cæcum). According to the observations of Fülleborn, the larvæ, on hatching, bore into the wall of the gut, and reach the liver almost

exclusively by way of the blood-stream. They do not, apparently, pass through the lungs. It is not known how the eggs normally leave the liver of the host, and it is not certain that they escape with the fæces. They do not, however, appear to be capable of reaching the infective stage in the liver, so that cannibalism on the part of rats does not seem to be an adequate explanation of the spread of infection. Under experimental conditions eggs removed from the liver develop very slowly. Both Bancroft and Railliet found that segmentation only began after three months, while the embryos were not formed until after five or six months. The embryos in eggs kept in water have been found to live for considerably over two years.

The genus **Eucoleus** Dujardin, 1845, was erected for a species, **E. aerophilus** (Creplin, 1839), found in the trachea of the fox, and recorded also from the cat, dog, wolf and badger, and a second species found in the hedgehog. There seem to be no characters to separate *Eucoleus* definitely from *Hepaticola*, except the presence of dorsal and ventral bacillary bands in the former, and their supposed absence in the latter. It seems not improbable, in fact, as Yorke and Maplestone have suggested, that *Hepaticola* should be regarded as a synonym of *Eucoleus*. In *Eucoleus*, as in *Hepaticola*, the male has no spicule, but a spicule-sheath is present, armed with minute spines. The eggs, when laid, are held together by a mucilaginous secretion, and may adhere to the body of the female.

In *E. aerophilus* the male is 24.5 mm. long, the female 32 mm. The œsophageal portion measures 8.3 mm. in the male and 7.4 mm. in the female. The spicule-sheath has twelve to fourteen longitudinal rows of spines on the protruded portion, and twenty-four rows on the non-protruded portion. The eggs measure 0.079 mm. in length, including the plugs, or 0.068 mm. without the plugs, and 0.035 mm. in width. The shell appears granulated.

ii. THE ACANTHOCEPHALA, OR THORNY-HEADED WORMS.

The Acanthocephala are an isolated group of worms, all of which are parasitic, as adults, in the alimentary canal of vertebrates. They are frequently regarded as being in some way related to the Nematoda, and forming part of a phylum Nemathelminthes. In reality, however, their affinities are extremely obscure, and their resemblance to the Nematoda is practically confined to the possession of a somewhat similar cuticle, a body-cavity and, in most cases, a cylindrical form.

The most striking peculiarity of the group is the absence of an alimentary canal of any kind. There is no mouth, and the only external aperture is that of the genital organs. This is situated at what is

generally regarded as the posterior end of the body. At the opposite, or anterior, end there is a "proboscis," serving as an organ of attachment to the host's tissues. This proboscis is a cylindrical, oval or rounded, hollow structure, armed (except in one genus) with posteriorly-directed hooks. The hooks are generally spoken of as being arranged in rows, both longitudinal and transverse, the hooks of adjacent rows alternating so that the arrangement is quincuncial. It would perhaps be more accurate in some cases to speak of them as being arranged in rows which pass obliquely or in a very open spiral from the apex of the proboscis towards its base. For the purpose of counting the hooks, however, a process which is often necessary in the determination of species, the usual conception is more convenient.

The outer layer of the body-wall consists of a tough, elastic cuticle, composed of several strata, and sometimes armed in certain regions with spines. These are of a similar nature to the hooks of the proboscis, and do not form part of the external layer of the cuticle itself, but are implanted in it by means of a more or less expanded root-like portion. Below the cuticle there is a subcuticular layer consisting of a nucleated tissue in which cell-boundaries are not distinguishable (syncytium). The nuclei in this layer, and indeed in all the tissues, are comparatively few and often very large. Branching capillary vessels may often be observed in the subcuticular layer. These contain a fluid, but their function is not understood, and it is not known whether they are concerned in excretion or in the absorption of food. The musculature of the body lies below the subcuticular layer, and is composed of an outer layer of circular and a less well developed inner layer of longitudinal fibres.

The muscles, as in the nematodes, are in immediate contact with the fluid with which the body-cavity is tensely filled, and in which the internal organs are suspended.

At the anterior end of the body a cylindrical, muscular sac, the proboscis-sac or receptacle of the proboscis, hangs into the cavity. Into this the proboscis can be invaginated by means of four retractor muscles which pass through the walls of the sac to their insertion in the body-wall. The evagination of the proboscis is effected by the contraction of the walls of the sac, which increases the pressure of the contained fluid. At the sides of the proboscis-sac, and connected with the base of the proboscis, but with their ends hanging freely, there is a pair of sac-like, nucleated organs known as the lemnisci. These may be concerned in the secretion or storage of the fluid of the proboscis and its sac.

The central ganglion of the nervous system is situated in the proboscis-sac, and gives off nerves to the proboscis and to the body. No special sense-organs are known. The only excretory organs described

are a pair of branching nephridia projecting into the body-cavity near the posterior end, their terminal branches being perforated and containing bunches of vibratile cilia. The ducts of these nephridia unite into a dorsal canal which opens into the vagina in the female, or into the ejaculatory duct in the male.

Attached to the posterior end of the proboscis-sac, and running back to the hinder end of the body, is a "suspensory ligament" in connection with which the genital organs are developed. The sexes are separate. The male has a pair of testes, oval or elongate in form and generally arranged in "tandem" formation. Behind these, and connected with the ejaculatory duct, there are several pairs of "cement-glands" or "prostatic glands." The ejaculatory duct opens into a protrusible "bursa copulatrix" which, when evaginated, forms a bell-like structure at the posterior end of the body. In the female the gonad discharges its ova in masses (called "swimming ovaries") into the body-cavity, and here the fertilization of the ova takes place, as well as the initial stages of development. Connected with the posterior end of the "ligament" and with the vagina is a remarkable structure called the "bell." This organ has a wide opening anteriorly, and "swallows" eggs contained in the fluid of the body-cavity. Immature ova, not yet surrounded by their shells, are returned to the body-cavity by a small aperture near the posterior end of the bell, while mature eggs, enclosed in shells, are passed on into the vagina.

The fully-formed egg is enclosed in a shell composed of three or four envelopes, successively secreted by the embryo. The latter, when it has reached the final stage of its development, is armed at one end with a number of chitinoid spines. The eggs reach the exterior with the fæces of the host, and the development of the embryos depends upon their being ingested by a suitable intermediate host. It is not certain whether in all cases the first intermediate host is an invertebrate. This is certainly the case with many species, and in some no other intermediate host is required. In other cases, however, the larval forms are found encapsuled in the body-cavity, serous membranes or viscera of vertebrate animals, and it is not known whether these are directly infected by means of eggs, or indirectly by devouring an invertebrate host containing an earlier larval stage.

Between thirty and forty genera of Acanthocephala are at present recognized. The classification of these into families and higher groups is a matter of some difficulty, owing to the rather slight characters upon which such classification must be based. No general agreement appears yet to have been reached by specialists on this group, and for our present purpose it will, perhaps, be sufficient to adhere to a somewhat con-

servative system of classification, in which the species with which we are immediately concerned will fall into two families only.

ECHINORHYNCHIDÆ.

In the family **Echinorhynchidæ** (*sens. lat.*) the males possess six cement-glands, and the hooks of the proboscis have but a single (posterior) root.

The genus **Polymorphus** Lühe, 1911, consists of small forms in which the body is covered in the anterior region with fine spines, and surrounded, behind the spiny portion, by an annular constriction. The proboscis is moderately long and armed with numerous hooks. The proboscis-sac has a double wall, and is inserted at the base of the proboscis. There is a long "neck," which is invaginable even when the proboscis is not invaginated. The lemnisci are moderately long and flattened. The testes are oval and situated in the anterior half of the body. The cement-glands are elongate. The eggs are narrow and fusiform, being about five times as long as broad. The middle shell of the egg has a prolongation at each pole.

Polymorphus boschadis (Schrank, 1788) (= *Echinorhynchus minutus* Zeder, 1800) is a form occurring in the intestine of the duck, fowl, swan and various wild aquatic or semi-aquatic birds. It is of an orange-red colour when fresh. The male measures about 3 mm. in length and 0.65 to 0.85 mm. in thickness, the female being much larger (up to 10 mm. long). The proboscis has sixteen longitudinal rows each of seven to ten hooks. The eggs measure 0.09 to 0.11 × 0.018 to 0.019 mm. The larval form of this species occurs in the fresh-water "shrimp," *Gammarus pulex*, and perhaps also in the crayfish, *Potamobius astacus*.

In the genus **Filicollis** Lühe, 1911, the body is narrow and cylindrical, and there is a long "neck." The proboscis, in the female, is swollen into a globular expansion, with the hooks arranged in radiating rows on a small area at the pole. In the male it is much less highly developed,

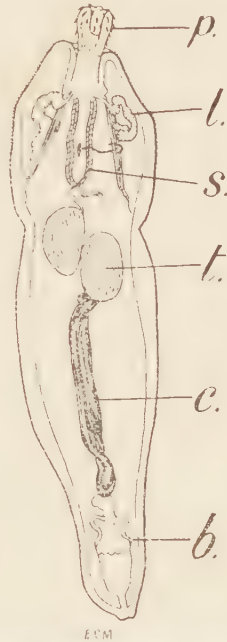


FIG. 197.—*Polymorphus boschadis*: MALE. (AFTER LÜHE.)

b., bursa copulatrix; c., cement-glands; l., lemniscus; p., proboscis; s., proboscis-sac; t., testis.

of oval shape and somewhat wider than the neck, with the hooks normally arranged upon it. The cuticle of the body, in the male, bears a number of small spines for a short distance behind the "neck." The proboscis-sac is long and slender, has a double wall, and is inserted at the base of the proboscis. In the mature female it lies entirely in the "neck." The lemnisci are very long and cylindrical. The testes are oval and lie in the middle third of the body. The cement-glands are large, irregularly oval and closely crowded together. The eggs are oval, and only about twice or three times as long as broad. The middle shell is without polar prolongations.

Filicollis anatis (Schrank, 1788) (= *Echinorhynchus filicollis* Rudolphi, 1804) occurs in the duck, swan and many wild aquatic or semi-aquatic



FIG. 198.—*Filicollis anatis*. (AFTER LÜHE.)

A, anterior end of male; B, anterior end of female, less highly magnified.

birds. The proboscis and neck of the female are completely buried in the wall of the host's intestine, so that the proboscis lies immediately below the peritoneal covering, and forms a conspicuous nodule on the exterior. The male is white and measures 6 to 8 mm. in length and about 1.4 mm. in thickness. The female is yellowish, 10 to 25 mm. long and up to 4 mm. thick. In the male the proboscis is about 0.36 mm. long and 0.28 mm. thick. In the female it is 2 to 3 mm. in diameter. The hooks are in eighteen to twenty-two longitudinal rows of ten to eleven each. The eggs measure 0.056 to 0.07 × 0.019 to 0.03 mm.

Corynosoma strumosum (Rudolphi, 1802), a form in which the anterior portion of the body is considerably expanded and covered with spines, is normally a parasite of seals and of cormorants, its larval form occurring in fishes. It has been recorded once (doubtless as an accidental infection) in the stomach of the cat.

In **Centrorhynchus** Lühe, 1911, the proboscis-sheath is inserted near the middle of the proboscis. The hooks behind the insertion are simple and thorn-like. Anteriorly to it they are powerful, with recurved roots. The species generally occur in birds.

Immature specimens found once in the small intestine of the cat in India have been referred to this genus by Chandler (1925) and named by him **C. erraticus**. These specimens were 7.5 to 8.5 mm. long. The anterior portion of the body was oval, and markedly thicker (1.2 to 1.4 mm.) than the posterior portion (0.425 to 0.5 mm.). The proboscis was 1.1 to 1.2 mm. long and 0.39 to 0.425 mm. thick, and bore forty-three transverse rows of about eighteen hooks each, of which the largest measured 0.055 to 0.065 mm. in length.

Immature forms found in a cat have also been referred by Kostylev (1926) to *Centrorhynchus aluconis* (Müller, 1780), a species normally parasitic in owls, hawks and other birds. The larval form of this species is found in amphibia and reptiles, and the infection of the cat was probably accidental.

In **Plagiorhynchus** Lühe, 1911, the body is usually short and stout, and sometimes ovoid in shape. The proboscis is cylindrical, and armed with numerous hooks. The proboscis-sac is double-walled and inserted at the base of the proboscis.

P. formosus Van Cleave, 1918, a form occurring in various passerine birds, has recently been recorded twice from the fowl in America. The specimens found in chickens were small and immature, and the infections may have been merely accidental. Full-grown males may be 8.5 mm. long, females 9.5 mm. In both sexes the maximum thickness is 2 mm. There are sixteen longitudinal rows of thirteen to fourteen hooks, measuring 0.065 to 0.083 mm. in length. The testes are in the anterior region of the body, and the cement glands are long and tubular. The eggs measure 0.048 to 0.06×0.012 to 0.02 mm.

GIGANTORHYNCHIDÆ.

In the family **Gigantorhynchidæ** (*sens. lat.*) the males have eight cement-glands. The proboscis is usually non-retractile in the adult, and armed with comparatively few rows of hooks. The latter have, as

a rule, double roots (an anterior and a posterior root-process), though in some cases the root is single.

The genus *Macracanthorhynchus* Travassos, 1916, contains rather large forms in which the proboscis is almost globular and bears stout hooks having double roots. The body of the male is usually curved into the shape of a comma, while that of the female tends to be spirally curled. The body, especially in the female, is considerably thicker in the anterior region than posteriorly. There is a conical "neck," without spines. The lemnisci are relatively short and flattened. The testes are elongate and situated in the anterior half of the body.

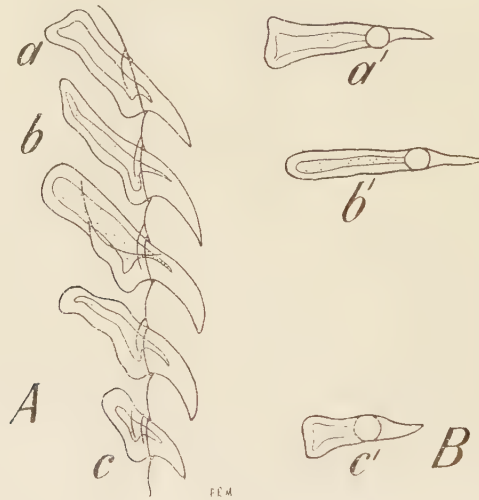


FIG. 199.—*Macracanthorhynchus hirudinaceus*: HOOKS FROM PROBOSCIS.
(AFTER TRAVASSOS.)

A, in profile; B, in surface view.

The cement-glands are oval and arranged in pairs, and are situated at some distance from the posterior testis. The eggs are oval and have four envelopes, of which the second is irregularly pitted and brownish, while the innermost is a thick, transparent shell.

M. hirudinaceus (Pallas, 1781) (= *Echinorhynchus gigas* Bloch, 1782; *Gigantorhynchus gigas* Hamann, 1892) is a parasite of the pig, and is widely distributed and fairly common in some countries. It occurs also in the wild boar, various carnivores and monkeys, and is said to occur in man in Russia. It inhabits the small intestine, especially the duodenum, and less commonly the large intestine. The male measures 50 to 100 mm. in length, and 3 to 5 mm. in maximum thickness. The female is 100 to 360 mm. long, or even, occasionally, as much as 475 mm., and 4 to 10 mm.

thick. The proboscis is about 1 mm. long and 0.5 mm. in diameter, and the hooks are arranged in five or six transverse rows of six each (or twelve longitudinal rows of three each). These diminish in size from the anterior to the posterior rows, and the largest have a length of 0.432 mm., measured from the end of the anterior root to the point. The lemnisci are about 15 mm. long in the male, and 20 mm. in the female. The eggs measure 0.08 to 0.11×0.051 to 0.056 mm.

The intermediate hosts of this species are various beetles and their larvæ (including, in Europe, the cockchafer, *Melolontha melolontha*, and the rose chafer, *Cetonia aurata*; in North America, *Lachnosterna arcuata* and *Xyloryctes satyrus*; in South America *Diloboderus abderus*, *Phanæus splendidulus* and *Gromphas lucordairei*). The larvæ of the beetles become infected while feeding in manure-heaps or in soil contaminated with the eggs, and the larvæ become encysted in the body-cavity. The final hosts become infected by eating the grubs or pupæ, or the adult beetles.

A very closely related species from the dog has recently been described by Kostylev (1927) under the name of **Macracanthorhynchus catulinus**. It appears to be fairly common in Turkestan. This form measures 45 to 65 mm. in length in the male, 50 to 125 mm. in the female. The proboscis measures up to 0.53 mm. in length and the same in width, and has six transverse rows of hooks (or twelve longitudinal rows of three each). The length of the largest hooks (from the end of the anterior root to the point) is 0.22 to 0.242 mm. The eggs measure 0.092 to 0.105×0.0462 mm.

The genus **Oncicola** Travassos, 1916, consists of rather small species with a body of elongate-pyriform shape, somewhat flattened and wrinkled. The proboscis has a small number of stout hooks with double roots, the posterior roots being very small. The "neck" is without spines. The lemnisci are relatively very large. The testes are rounded and relatively small, and are situated in the anterior half of the body. The cement-glands are large and closely packed together. The adult worms occur in the stomach and intestine of carnivorous mammals.

Oncicola canis (Kaupp, 1909) is a species recorded from the intestine of the dog in North America (Texas and Nebraska). No detailed description of the worm appears to be available, but the female is said to be about half an inch long, the male somewhat smaller. The proboscis is globular and armed with six alternating rows of hooks. The dog in which this worm was first found died after exhibiting rabies-like symptoms, and on autopsy was found by Parker to have about 300 of the worms in the small intestine. The immediate cause of its death was said to have

been acute pulmonary congestion, but the signs of "madness" were attributed to the presence of the worms, and the interesting suggestion was made by Parker that *O. canis* is normally a parasite of the coyote or prairie wolf, since "mad" coyotes had been frequently reported in the vicinity. Van Cleave has recorded the occurrence of larval forms, believed to belong to this species, in the armadillo. The larval form of *O. oncocerca*, a species found in South American Felidæ, has also been recorded from the connective tissue and muscles of an armadillo (*Tatus* sp.). It appears likely, therefore, that dogs and coyotes might both acquire infection by preying upon armadillos.

In **Echinopardalis** Travassos, 1918 (= *Pardalis* Travassos, 1917, preoccupied) a "neck" is absent, the lemnisci are very long, the testes elongate and situated in the middle third of the body, and the cement-glands ovoid, arranged in pairs and close to the posterior testis. The adults occur in the intestine of Felidæ.

E. pardalis (Westrumb, 1821) (= *Echinorhynchus campanulatus* Diesing, 1851; *E. ovatus* Leidy, 1851, not Zeder, 1800) is a form occurring in various wild Felidæ in America, and recorded once from the domestic cat in the United States. The worm is 30 to 40 mm. long and 1 to 2.5 mm. thick, and has a stout proboscis armed with five or six transverse rows of hooks. The anterior hooks have double roots, and the largest measure 0.3 mm. in length. The lemnisci are about one-third the length of the body. The eggs measure 0.053 to 0.063 × 0.038 to 0.042 mm.

In the genus **Moniliformis** Travassos, 1915, the body usually has a moniliform appearance owing to a series of swellings or annular thickenings of its wall. There is no "neck." The proboscis is subcylindrical and retractile, and bears numerous small hooks having single, posteriorly-directed roots. The proboscis-sac is inserted at the base of the proboscis, and its wall is double, the outer layer consisting of stout, diagonally arranged muscular bands. The lemnisci are long and filiform. The testes are ellipsoidal and posteriorly situated.

M. moniliformis (Bremser, in Rudolphi, 1819) is normally a parasite of rodents (rats, mice and squirrels), but appears to occur occasionally (perhaps only accidentally) in the dog, and to be capable of infecting man.* The writer has also seen specimens which were obtained from a chimpanzee. It has a wide geographical range, having been recorded from

* The inclusion of this species among the parasites of man appears to be due to an experiment of Calandruccio's, in which he successfully infected himself with it.

Southern Europe, Africa, South America and Australia. The male measures 40 to 80 mm. in length, the female 70 to 110 mm. The maximum thickness is about 1 to 1.5 mm. The proboscis has fourteen longitudinal rows of about fifteen hooks each. These measure 0.024 to 0.028 mm. in length. The dimensions of the eggs are given by different authors as 0.085×0.045 and 0.124 to 0.127×0.071 to 0.074 mm.

According to Grassi and Calandruccio, the intermediate host of this species, in Europe, is a beetle, *Blaps mucronata*. The usual intermediate host, however, as has been shown by many observers, is the cockroach, *Periplaneta americana*.

"*Echinorhynchus*" *grassii* Railliet, 1893, a species based on a record by Grassi and Calandruccio of an Acanthocephalan found in a dog in

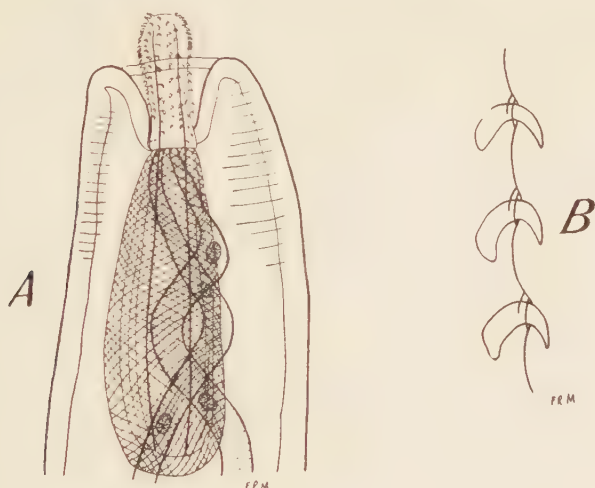


FIG. 200.—*Moniliformis moniliformis*. (AFTER TRAVASSOS.)

A, anterior end; B, hooks from proboscis, in profile.

Sicily, is probably a synonym of *M. moniliformis*. Kostylev (1927) has expressed the opinion that "*Echinorhynchus*" *canis* Porta, 1914, a form also found in a dog, in Belgium, was also *M. moniliformis*. This, however, seems rather more doubtful. In any case, the record of *E. canis* refers only to a single immature female specimen, and the description is insufficient to establish its position. The worm was 29 mm. long, with a cylindrical body, thickened anteriorly, a very short, unarmed neck, and an ovoid proboscis 0.4 mm. long and bearing eleven transverse series of hooks, of which the more anterior were powerful.

"*Echinorhynchus*" *hominis* Leuckart, 1876, is likewise of uncertain position. The species was based on a single immature female worm found

by Lambl in the small intestine of a boy at Prague in 1857. The worm was 5.6 mm. long and 0.6 mm. thick. It had a short, rounded proboscis, 0.36 mm. long and 0.34 mm. wide, and armed with eight alternating longitudinal rows of twelve hooks each. The length of the hooks, measured along the outer curve, was 0.1032 mm. The proboscis-sac was 0.64 mm. long. According to some authors, *E. hominis* is a synonym of *Macracanthorhynchus hirudinaceus*, but the arrangement, number and size of the hooks do not seem to support this view.

ADDENDA

It is impossible to ensure the completeness, up to the date of publication, of a work such as this, and it is probable that a number of species have been omitted, owing to the difficulty of seeing all the literature. An important list of parasites occurring in man and domestic animals in Indo-China, published by Professor A. Railliet in 1925 (*Bull. Soc. Zool. France*, XLIX., pp. 589-608, and L., pp. 7-26), has come to the author's notice too late for adequate treatment. This paper includes short descriptions of three new species of Trematodes, the more important features of which may be briefly given here.

Prosthogonimus fureifer, from bursa Fabricii of fowl. Size 8.2×5.7 mm. Suckers subequal, about 1 mm. in diameter. Intestinal cæca reaching anterior quarter of body, very conspicuous, forming a fork. Vitellaria extending from anterior border of ventral sucker to behind testes, and arranged in two fields on each side, of which the anterior is the larger.

Eurytrema rebelle, from pancreatic ducts of dog. Length 8 mm. Ventral sucker conspicuously larger than oral sucker. Testes at level of posterior part of ventral sucker, slightly lobate. Cirrus-sac reaching middle of ventral sucker. Eggs 0.046 to 0.052×0.028 to 0.035 mm.

Harmostomum annamense, from intestine of fowl. Size up to 6.5×1.8 mm. Oral sucker 0.75 mm. long $\times$ 0.975 mm. wide, with rounded aperture. Ventral sucker elliptical, transversely elongate, 0.53 mm. long $\times$ 0.67 mm. wide. Pharynx 0.48×0.44 mm. Genital pore in front of anterior testis. Vitellaria in an uninterrupted field laterally to the intestinal cæca, extending from posterior edge of ventral sucker to genital pore. Eggs 0.026×0.018 mm.

INDEX

TO PARASITES OF MAN AND PRINCIPAL DOMESTIC ANIMALS, ARRANGED UNDER THEIR HOSTS

MAN

TREMATODES:

- Dicrocoelium dendriticum*, 15
- Opisthorchis felineus*, 18
 - viverrini*, 19
 - noverca*, 19
- Clonorchis sinensis*, 20
- Pseudamphistomum truncatum*, 22
- Heterophyes heterophyes*, 23
 - katsuradai*, 24
- Metagonimus yokogawai*, 25
- Stamnosoma armatum*, 26
 - formosanum*, 26
- Monorchotrema taihokui*, 26
 - taichui*, 26
- Paragonimus westermanii*, 27
 - ringeri*, 27
- Fasciola hepatica*, 31
 - gigantica*, 31
- Fasciolopsis buskii*, 33
- Echinostoma ilocanum*, 40
- Euparyphium malayanum*, 41
 - sufrartyfex*, 42
 - jassyense*, 42
- Echinochasmus perfoliatus* var. *japonicus*, 43
- Schistosoma hamatobium*, 47
 - mansoni*, 48
 - japonicum*, 49
 - spindalis* var. *africana*, 50
 - incognitum*, 51
- Pseudodiscus watsoni*, 58
- Gastrodiscus hominis*, 62

CESTODES:

- Diphyllobothrium latum*, 68, 69
 - cordatum*, 68, 71
 - mansoni*, 68, 72
 - parvum*, 71
- Sparganum* (Gatesius) *proliferum*, 72
- Diplogonoporus grandis*, 74
 - brauni*, 74
- Braunia jassyensis*, 75
- Bertiella studeri*, 81
- Raillietina madagascariensis*, 92
 - asiatica*, 92
 - formosana*, 93
- Dipylidium caninum*, 99, 101
- Hymenolepis nana*, 103
 - diminuta*, 105
 - lanceolata*, 107, 108
- Tenia solium* (incl. *Cysticercus cellulosæ*), *

111

CESTODES—continued:

- Tania saginata*, 113
 - africana*, 114
 - hominis*, 114
 - confusa*, 114
 - tonkinensis*, 114
 - philippina*, 114
 - bremneri*, 114
 - infantis*, 114
- Cœnurus cerebralis*, 116
- Multiceps glomeratus*, 116
- Echinococcus granulosus*, 117

NEMATODES:

- Ascaris lumbricoides*, 129
 - texana*, 132
 - maritima*, 132
- Toxocara mystax*, 133
- Toxascaris limbata*, 133
- Lagochilascaris minor*, 134
- Oxyuris incognita*, 141
- Enterobius vermicularis*, 142
- Syphacia obvelata*, 143
- Strongyloides stercoralis*, 145
- Esophagostomum apiostomum*, 158, 159
 - brumpti*, 158, 159
 - stephanostomum* var. *thomasi*, 158, 159
- Ternidens deminutus*, 159
- Syngamus kingi*, 163
- Ancylostoma duodenale*, 164
 - braziliense*, 164
 - caninum*, 164
- Necator americanus*, 166
- Metastrongylus apri*, 172
- Trichostrongylus colubriformis*, 180
 - vitrinus*, 178, 179, 180
 - probolurus*, 180
 - extenuatus*, 178, 179, 180
 - orientalis*, 181
- Mecistocirrus digitatus*, 197, 198
- Dirofilaria immitis*, 207
- Acanthocheilonema perstans*, 208
- Wuchereria bancrofti*, 210
- Onchocerca volvulus*, 212
 - cæcutiens*, 212
- Setaria equina*, 216
- Loa loa*, 218
- Filaria ozzardi*, 219
 - taniguchii*, 219
 - [*Loa*] *extraocularis*, 219
 - conjunctivæ*, 220

NEMATODES—*continued*:

- Agamofilaria oculi, 220
 - palpebralis, 220
 - georgiana, 220
 - eiseni, 220
- Microfilaria powelli, 221
 - philippinensis, 221
 - romanorum, 221
 - nuda, 221
 - tucumana, 221
 - [Agamofilaria] streptocerca, 221
 - malayi, 221
- Dracunculus medinensis, 222
- Gongylonema pulchrum, 233
- Physaloptera caucasica, 242, 243
- Thelazia callipæda, 246
- Gnathostoma spinigerum, 250
 - hispidum, 252
- Diectophyme renalis, 253
- Trichinella spiralis, 256
- Trichuris trichiura, 258
- Hepaticola hepatica, 265

ACANTHOCEPHALA:

- Macracanthorhynchus hirudinaceus, 272
- Moniliformis moniliformis, 274
- Echinorhynchus hominis, 275

DOG

TREMATODES:

- Lepoderma massino, 12
- Dicrocoelium dendriticum, 15
- Eurytrema rebelle, 276
- Opisthorchis felineus, 18
 - caninus, 19
 - noverca, 19
- Clonorchis sinensis, 20
- Pseudamphistomum truncatum, 22
- Heterophyes heterophyes, 23
 - æqualis, 24
 - dispar, 24
- Rossicotrema venustum, 24
 - donicum, 24
- Nanophyetus salmincola, 25
- Metagonimus yokogawai, 25
- Cryptocotyle lingua, 26
- Centrocestus cuspidatus var. caninus, 26
- Stamnosoma formosanum, 26
- Ascoctyle minuta, 26
 - italica, 26
- Monorchotrema taihokui, 26
 - taichui, 26
- Paragonimus westermanii, 27
 - kellicotti, 28
- Echinochasmus perfoliatus, 43
- Schistosoma japonicum, 49
- Prohemistomum appendiculatum, 53
 - industrium, 54
- Alaria alata, 54
 - americana, 54
 - michiganensis, 54

CESTODES:

- Dipyllobothrium latum, 68, 69
 - cordatum, 68, 71
 - fuscum, 68

CESTODES—*continued*:Dipyllobothrium—*continued*:

- decipiens, 68
- mansoni, 68, 72
- raillieti, 68
- reptans, 68
- ranarum, 68
- americanum, 68
- Mesocestoides lineatus, 78
 - litteratus, 78
- Cysticercus elongatus (= Dithyridium bailleti), 79
- Anoplocephala sp., 81
- Dipylidium caninum, 99, 101
 - sexocoronatum, 100, 101
 - walkeri, 101
 - rossicum, 101
 - gracile, 101
 - crassum, 101
 - buencaminoi, 101
- Cysticercus cellulosæ, 112
- Tænia antarctica, 115
 - balaniceps, 115
 - brachysoma, 115
 - brauni, 115
 - hydatigena, 115, 116
 - krabbei, 115, 116
 - ovis, 115, 116
 - pisiformis, 115
 - multiceps, 115
 - serialis, 115
 - gaigeri, 115
- Echinococcus granulosus, 117

NEMATODES:

- Ascaris lumbricoides, 129
- Toxocara canis, 133
- Toxascaris limbata, 133
- Enterobius vermicularis (?), 142
- Strongyloides stercoralis, 145
- Ancylostoma braziliense, 164
 - caninum, 164
- Necator americanus, 166
- Uncinaria stenocephala, 165, 170
- Angiostrongylus vasorum, 177
- Oslerus osleri, 177
- Dirofilaria immitis, 206
 - repens, 207
- Acanthocheilonema dracunculoides, 209
 - reconditum, 209
 - grassii, 209
- Microfilaria auquieri, 221
 - lewisii, 221
- Dracunculus medinensis, 222
- Spirocerca sanguinolenta, 231
 - arctica, 232
- Physaloptera rara, 244
- Thelazia callipæda, 246
- Rictularia cahirensis, 249
- Gnathostoma spinigerum, 250
- Diectophyme renalis, 253
- Trichinella spiralis, 256
- Trichuris vulpis, 259, 260
- Capillaria plica, 263
- Hepaticola hepatica (?), 265
- Eucolus aerophilus, 266

ACANTHOCEPHALA:

- Macracanthorhynchus catulinus, 273
- Oncicola canis, 273
- Moniliformis moniliformis, 274
- Echinorhynchus canis, 275

CAT

TREMATODES:

- Lepoderma massino, 12
- Platynosomum fastosum, 16
- Opisthorchis felineus, 18
 - wardi, 19
 - pseudofelineus, 19
- Clonorchis sinensis, 20
- Metorchis albidus, 21
- Parametorchis complexus, 21
 - noveboracensis, 21
- Pseudamphistomum truncatum, 22
 - danubiense, 22
- Heterophyes heterophyes, 23
 - continuus, 24
 - æqualis, 24
 - dispar, 24
- Rossicotrema venustum, 24
- Metagonimus yokogawai, 25
- Ascocotyle minuta, 26
- Monorchotrema taihokui, 26
 - taichui, 26
- Paragonimus westermanii, 27
 - kellicotti, 28
- Echinochasmus perfoliatus, 43
- Schistosoma japonicum, 49
- Prohemistomum appendiculatum, 53
- Alaria alata, 54
 - americana, 54
- Pharyngostomum cordatum, 55

CESTODES:

- Diphyllobothrium latum, 68, 69
 - decipiens, 68
 - mansonii, 68, 72
- Mesocostoides lineatus, 78
- Cysticercus elongatus (= Dithyridium bailleti), 79
- Dipylidium caninum, 99, 101
 - oerleyi, 101
 - sexcoronatum, 100, 101
 - gracile, 101
 - compactum, 101
 - diffusum, 101
 - longulum, 101
 - halli, 101
- Joyeuxia chyzeri, 101, 102
 - pasqualei, 101
- Diplopylidium trinchessii, 101, 102
 - quinquecoronatum, 101
 - nölleri, 101
- Cysticercus cellulosæ, 112
- Tænia tæniæformis, 115, 116
 - pisiformis, 115, 116
 - novella, 115
 - hydatigena (?), 115, 116
- Echinococcus granulosus, 117

NEMATODES:

- Toxocara mystax, 133
- Toxascaris leonina, 133

NEMATODES—continued:

- Oxyuris compar, 141
- Strongyloides stercoralis, 145
- Ancylostoma braziliense, 164
- Ælurostrongylus abstrusus, 176
- Ollulanus tricuspis, 198
- Dirofilaria immitis, 206
- Cylicospirura subæqualis, 233
- Physaloptera præputialis, 243
 - gemina, 244
 - pacitæ, 244
- Rictularia cahirensis, 249
- Gnathostoma spinigerum, 250
- Trichinella spiralis, 256
- Trichuris serrata, 260
 - campanula, 260
- Capillaria linearis, 263
 - felis-cati, 263
- Eucoleus aerophilus, 266

ACANTHOCEPHALA:

- Corynosoma strumosum, 271
- Centrorhynchus erraticus, 271
 - aluconis, 271
- Echinopardalis pardalis, 274

PIG

TREMATODES:

- Dicrocoelium dendriticum, 15
- Opisthorchis felineus, 18
- Clonorchis sinensis, 20
- Microtrema truncatum, 22
- Metagonimus yokogawai, 25
- Paragonimus westermanii, 27
 - kellicotti, 28
- Fasciola hepatica, 31
- Fasciolopsis buskii, 33
- Euparyphium suinum, 42
- Echinochasmus perfoliatus, 43
- Testifrons cristata, 44
- Cladorchis giganteus, 59
- Gastrodiscus ægyptiacus, 61
 - minor, 61
 - hominis, 62

CESTODES:

- Sparganum railletii, 72
- Helicometra giardi (?), 89
- Cysticercus cellulosæ, 112
 - tenuicollis, 116
- Cœnurus cerebralis, 116
- Echinococcus granulosus, 117

NEMATODES:

- Ascaris lumbricoides, 129
- Strongyloides papillosus, 145
 - westeri, 145
- Bourgelatia diducta, 157
- Æsophagostomum dentatum, 158
 - longicaudum, 158
- Stephanurus dentatus, 160
- Ancylostoma duodenale, 164, 165
- Necator americanus, 166
 - suillus, 166

NEMATODES—*continued*:

- Globocephalus longemucronatus, 167
- samoensis, 167
- urosululatus, 167
- amucronatus, 168
- Metastrongylus apri, 171, 172
- salmi, 172
- Chærostrongylus pudendotectus, 172, 173
- Hyoststrongylus rubidus, 183
- Mecistocirrus digitatus, 197, 198
- Setaria bernardi, 218
- Arduenna strongylina, 228
- dentata, 229
- Simondsia paradoxa, 229
- Physocephalus sexalatus, 230
- Gongylonema pulchrum, 233
- Gnathostoma hispidum, 252
- doloresi, 252
- Diectophyme renalis, 253
- Trichinella spiralis, 256
- Trichuris trichiura, 258

ACANTHOCEPHALA:

- Macracanthorhynchus hirudinaceus, 272

CATTLE (INCLUDING OX, ZEBU AND BUFFALO)

TREMATODES:

- Dicrocoelium dendriticum, 15
- hospes, 15
- Eurytrema pancreaticum, 17
- cœlomaticum, 17
- parvum, 17
- dajii, 17
- Paragonimus westermanii, 27
- Fasciola hepatica, 31
- gigantica, 31
- magna, 32
- Schistosoma japonicum, 49
- bovis, 49
- bomfordi, 49
- spindalis, 50
- türkistanicum, 51
- Paramphistomum cervi, 56
- anisocotylea, 56
- gotoi, 56
- ichikawai, 56
- explanatum, 57
- ijimai, 57
- orthocœlium, 57
- Cotylophoron cotylophorum, 57
- Balanorchis anastrophus, 58
- Stephanopharynx compactus, 59
- Gastrothylax crumenifer, 60
- Fischoederius elongatus, 60
- cobboldii, 60
- Carmyerius spatiosus, 61
- gregarius, 61
- Homalogaster paloniæ, 62

CESTODES:

- Moniezia expansa, 82
- benedeni, 83
- denticulata, 83
- Avitellina goughi, 86

CESTODES—*continued*:

- Thysanosoma actinioides, 89
- Helicometra giardi, 89
- Cysticercus cellulosæ, 112
- bovis, 113
- tenuicollis, 116
- Cœnurus cerebri, 116
- Echinococcus granulosus, 117

NEMATODES:

- Ascaris lumbricoides, 129
- equorum, 131
- vitulorum, 131
- Strongyloides papillosus, 145
- Cesophagostomum columbianum (?), 157, 158
- radiatum, 158, 159
- Chabertia ovina, 159
- Syngamus laryngeus, 162
- Agriostomum vryburgi, 165
- Bunostomum trigonocephalum, 168
- phlebotomum, 169
- Gaigeria pachyscelis (?), 169
- Dictyocaulus viviparus, 174
- Trichostrongylus extenuatus, 178, 179
- Cooperia punctata, 183
- oncophora, 183
- pectinata, 182, 183
- Ostertagia ostertagi, 185
- lyrata, 186
- Hæmonchus contortus, 190, 191, 192
- similis, 192
- lunatus, 193
- Nematodirus filicollis, 194
- spathiger, 194
- helveticus, 196
- Mecistocirrus digitatus, 197, 198
- Cordophilus sagitta, 211
- Onchocerca gibsoni, 213
- indica, 214
- gutturata, 214
- bovis, 214
- armillata, 214
- lienalis, 214
- Elæophora poeli, 215
- Setaria equina, 216
- labiato-papillosa, 216
- digitata, 217
- marshalli, 217
- Microfilaria guyanensis, 221
- Dracunculus medinensis, 222
- Parabronema skrjabini, 226
- Arduenna strongylina, 228
- Physocephalus sexalatus, 230
- Gongylonema pulchrum, 233
- verrucosum, 234, 235
- Thelazia rhodesii, 245
- gulosus, 246
- alfortensis, 246
- Gnathostoma hispidum (?), 252
- Diectophyme renalis, 253
- Trichinella spiralis, 256
- Trichuris ovis, 260, 261
- discolor, 261
- Capillaria bovis, 263

SHEEP

TREMATODES:

- Dicrocoelium dendriticum*, 15
- Platynosomum arietis*, 16
- Eurytrema pancreaticum*, 17
 - ovis*, 17
- Fasciola hepatica*, 31
 - gigantica*, 31
- Schistosoma bovis*, 49
 - indicum*, 50
- Paramphistomum cervi*, 56
 - orthocelium*, 57
- Cotylophoron cotylophorum*, 57
- Gastrothylax crumenifer*, 60

CESTODES:

- Moniezia expansa*, 82
 - benedeni*, 83
 - denticulata*, 83
- Avitellina centripunctata*, 85
 - sudanea*, 86
 - chalmersi*, 86
 - goughi*, 86
 - laciniosa*, 86
- Hexastichorchis pintneri*, 86
- Stilesia hepatica*, 87
 - globipunctata*, 88
- Thysanosoma actinioides*, 89
- Helicometra giardi*, 89
- Cysticercus cellulosæ*, 112
 - bovis*, 113
 - tenuicollis*, 116
 - ovis*, 116
- Cœnurus cerebralis*, 116
- Echinococcus granulosus*, 117

NEMATODES:

- Ascaris lumbricoides*, 129
- Skrjabinema ovis*, 143
- Strongyloides papillosus*, 145
- Esophagostomum columbianum*, 157, 158
 - venulosum*, 158
- Chabertia ovina*, 159
- Bunostomum trigonocephalum*, 168
 - phlebotomum*, 169
- Gaigeria pachyscelis*, 169
- Dictyocaulus filaria*, 173
- Protostrongylus rufescens*, 175
 - ocreatus*, 174, 175
 - unciphorus*, 175
 - linearis*, 175
- Muellerius capillaris*, 175
- Trichostrongylus extenuatus*, 178, 179
 - rugatus*, 179
 - vitrinus*, 178, 179, 180
 - probolurus*, 180
 - colubriformis*, 180
 - capricola*, 180
- Cooperia curticei*, 182, 183
 - onophora*, 183
- Ostertagia circumcincta*, 186
 - trifurcata*, 187
 - marshalli*, 187
 - tricuspis*, 187, 188
 - occidentalis*, 188
 - bullosa*, 188

NEMATODES—continued:

- Ostertagia—continued:*
 - turkestanica*, 188
 - mentulata*, 189
 - trifida*, 188
- Hæmonchus contortus*, 190, 191, 192
- Nematodirus filicollis*, 194
 - spathiger*, 194
 - abnormalis*, 194
 - furcatus*, 196
- Mecistocirrus digitatus*, 197, 198
- Parabronema skrjabini*, 226
- Gongylonema pulchrum*, 233
 - verrucosum*, 234, 235
 - monnigi*, 235, 236
- Trichinella spiralis*, 256
- Trichuris ovis*, 260, 261
- Capillaria brevipes*, 262
 - longipes*, 263

GOAT

TREMATODES:

- Dicrocoelium dendriticum*, 15
- Eurytrema pancreaticum*, 17
- Paragonimus westermanii*, 27
- Fasciola hepatica*, 31
 - gigantica*, 31
- Schistosoma japonicum*, 49
- Paramphistomum cervi*, 56
- Gastrothylax crumenifer*, 60

CESTODES:

- Moniezia expansa*, 82
 - benedeni*, 83
- Avitellina goughi*, 86
- Stilesia hepatica*, 87
 - globipunctata*, 88
- Cysticercus cellulosæ*, 112
 - bovis*, 113
 - tenuicollis*, 116
 - ovis*, 116
- Cœnurus cerebralis*, 116
- Cœnurus of Tænia gaigieri*, 116
- Cœnurus of (?) T. serialis*, 116
- Echinococcus granulosus*, 117

NEMATODES:

- Skrjabinema ovis*, 143
- Strongyloides papillosus*, 145
- Esophagostomum columbianum*, 157, 158
 - venulosum*, 158
 - asperum*, 158
- Chabertia ovina*, 159
- Syngamus nasicola*, 162
- Bunostomum trigonocephalum*, 168
- Gaigeria pachyscelis*, 169
- Dictyocaulus filaria*, 173
- Protostrongylus rufescens*, 175
 - unciphorus*, 175
- Muellerius capillaris*, 175
- Trichostrongylus extenuatus*, 178, 179
 - vitrinus*, 178, 179, 180
 - colubriformis*, 180
 - falculatus*, 180
 - capricola*, 180
- Cooperia curticei*, 182, 183

NEMATODES—*continued*:

- Ostertagia circumcincta*, 186
 - trifurcata*, 187
 - marshalli*, 187
 - turkestanica*, 188
 - mentulata*, 189
- Hæmonchus contortus*, 190, 191, 192
- Nematodirus filicollis*, 194
 - spathiger*, 194
 - abnormalis*, 194
- Filaria capræ*, 220
- Parabronema skrjabini*, 226
- Gongylonema pulchrum*, 233
- Trichuris ovis*, 260, 261

CAMEL

TREMATODES:

- Fasciola hepatica*, 31
- Schistosoma indicum*, 50

CESTODES:

- Stilesia vittata*, 88
- Cysticercus cellulosæ*, 112
- Echinococcus granulosus*, 117

NEMATODES:

- Æsophagostomum venulosum*, 158
- Dictyocaulus filaria*, 173
- Trichostrongylus vitrinus*, 178, 179, 180
 - probolurus*, 180
 - colubriformis*, 180
- Ostertagia mentulata*, 189
- Hæmonchus longistipes*, 193
- Nematodirus spathiger*, 194
 - mauritanicus*, 196
 - dromedarii*, 196
- Acanthocheilonema evansi*, 209
- Onchocerca fasciata*, 214
- Parabronema skrjabini*, 226
- Physocephalus sexalatus*, 230
 - cristatus*, 230
- Gongylonema pulchrum*, 233
- Thelazia leesei*, 247
- Trichuris ovis*, 260, 261
 - globulosa*, 261
 - cameli*, 261
 - skrjabini*, 261

HORSE TRIBE (INCLUDING HORSE, DONKEY AND MULE)

TREMATODES:

- Dicrocoelium dendriticum*, 15
- Fasciola hepatica*, 31
- Schistosoma japonicum*, 49
 - indicum*, 50
- Pseudodiscus collinsii*, 58
- Gastrodiscus ægyptiacus*, 61
 - secundus*, 61

CESTODES:

- Anoplocephala perfoliata*, 80
 - magna*, 80
 - mamillana*, 80
- Moniezia pallida*, 83
- Cysticercus cellulosæ*, 112
- Cœnurus cerebralis*, 116
- Cœnurus of Tænia serialis*, 116
- Echinococcus granulosus*, 117

NEMATODES:

- Ascaris equorum*, 131
- Probstmayria vivipara*, 139
- Oxyuris equi*, 141
 - poculum*, 141
- Strongyloides westeri*, 145
- Strongylus equinus*, 148, 149
 - edentatus*, 148, 149, 150
 - vulgaris*, 148, 149, 150
 - asini*, 148, 149, 150
- Triodontophorus serratus*, 150, 151
 - tenuicollis*, 151
 - brevicauda*, 151
 - minor*, 151
- Craterostomum acuticaudatum*, 151
 - mucronatum*, 151
- Æsophagodontus robustus*, 151
- Trichonema*—numerous species; see Table IX, p. 154, and pp. 152-156
- Poteriostomum imparidentatum*, 156
 - rátzii*, 156
- Gyalocephalus capitatus*, 156
- Acheilostoma paranecator*, 170
- Dictyocaulus arnfieldi*, 174
 - viviparus* (?), 174
- Trichostrongylus axei*, 181
- Parafilaria multipapillosa*, 205
- Onchocerca reticulata*, 213
 - cervicalis*, 213
- Setaria equina*, 216
 - digitata*, 217
- Filaria cordicola*, 220
 - spirovoluta*, 220
- "*Microfilaria sanguinis equi africana*," 221
- Dracunculus medinensis*, 222
- Habronema muscæ*, 223, 224
 - microstoma*, 224
 - megastoma*, 225
- Physocephalus sexalatus*, 230
- Gongylonema pulchrum*, 233
- Thelazia lacrymalis*, 246
- Diectophyme renalis*, 253
- Trichinella spiralis*, 256

FOWL

TREMATODES:

- Lepoderma arcuatum*, 12
- Prosthogonimus intercalandus*, 13
 - ovatus*, 13, 14
 - cuneatus*, 14
 - pellucidus*, 14
 - brauni*, 14
 - japonicus*, 14
 - furcifer*, 276
- Collyriclum faba*, 29
- Philophthalmus gralli*, 29
- Bunodera linearis*, 34
- Notocotylus attenuatus*, 37
- Catantropis verrucosa*, 38
- Echinostoma revolutum*, 39
 - paraulum*, 40
- Hypoderaum conoideum*, 40
- Echinoparyphium recurvatum*, 41
- Episthmium oscari*, 44
- Harmostomum commutatum*, 46
 - annamense*, 276

CESTODES:

- Anoplocephala minima*, 81
- Davainea proglottina*, 90
- Raillietina tetragona*, 93, 94
 - echinobothrida*, 92, 93, 94
 - mutabilis*, 74
 - volzii*, 94
 - cohnii*, 94
 - penetrans*, 94
 - grobbeni*, 94
 - birmanica*, 94
 - pseudoechinobothrida*, 94
 - cesticillus*, 93, 94
- Davainoides vigintivasus*, 95
- Cotugnia digonopora*, 95
- Amœbotenia sphenoides*, 97
- Choanotania infundibulum*, 97
- Southwellia gallinarum*, 98
- Metroliasthes lucida*, 102
- Hymenolepis cantaniana*, 106
 - exilis*, 106
 - villosa*, 106
 - tichodroma*, 106
 - inermis*, 106
 - exigua*, 106
 - pullæ*, 106
 - bauchei*, 106
 - carioca*, 106
 - rustica*, 106
 - fedtschenkowi*, 106
- Fimbriaria fasciolaris*, 110

NEMATODES:

- Heterakis gallinæ*, 135, 136
 - brevispiculum*, 136
 - beramporia*, 136
 - putaustralis*, 136
- Ascaridia perspicillum*, 137
 - lineata*, 137
 - compar*, 137
 - styphlocerca*, 138
 - compressa*, 138
 - granulosa*, 138
- Subulura (Alloodapa) differens*, 139
 - brumpti*, 139
- Syngamus trachea*, 161
- Trichostrongylus tenuis*, 181
- Microfilaria seguini*, 221
- Hartertia gallinarum*, 227
- Histioccephalus laticaudatus*, 227
- Gongylonema ingluvicola*, 236
- Acuaria (Cheilospirura) hamulosa*, 237
- Acuaria (Dispharynx) spiralis*, 238
 - nasuta*, 238
- Streptocara pectinifera*, 239
- Tropisurus fissispinus*, 240
 - confusus*, 241
 - americanus*, 241
 - gallineis*, 241
- Physaloptera gemina*, 244
 - truncata*, 244, 245
- Oxyspirura mansoni*, 247
 - parvovum*, 247
- Capillaria retusa*, 264
 - longicollis*, 264
 - annulata*, 264
 - caudinflata*, 264

NEMATODES—continued:

- Capillaria—continued:*
 - dubia*, 264
 - collaris*, 264
 - gallina*, 264
 - columbæ*, 264

ACANTHOCEPHALA:

- Polymorphus boschadis*, 269
- Plagiorhynchus formosus*, 271

TURKEY

TREMATODES:

- Collyriclum faba*, 29
- Cyclocœlum mutabile*, 35
- Harmostomum commutatum*, 46

CESTODES:

- Raillietina cesticillus*, 93, 94
- Metroliasthes lucida*, 102
- Hymenolepis meleagris*, 106
 - musculosa*, 106

NEMATODES:

- Heterakis gallinæ*, 135, 136
- Ascaridia perspicillum*, 137
- Subulura (Alloodapa) brumpti*, 139
- Syngamus trachea*, 161
- Trichostrongylus tenuis*, 181
- Acuaria (Cheilospirura) hamulosa*, 237
 - (Dispharynx) spiralis*, 238
- Tropisurus fissispinus*, 240
 - confusus*, 241
- Oxyspirura mansoni*, 247
- Capillaria annulata*, 264
 - meleagris-gallopavo*, 264
 - columbæ*, 264

GUINEA-FOWL

TREMATODES:

- Prosthogonimus cuneatus*, 14
- Dicrocoelium macrostomum*, 16
- Harmostomum commutatum*, 46

CESTODES:

- Raillietina tetragona*, 93, 94
 - cesticillus*, 93, 94

NEMATODES:

- Heterakis gallinæ*, 135, 136
- Ascaridia perspicillum*, 137
- Subulura (Alloodapa) differens*, 139
 - brumpti*, 139
- Acuaria (Dispharynx) spiralis*, 238
- Streptocara pectinifera*, 239
- Capillaria retusa*, 264

DUCK

TREMATODES:

- Lepoderma potanini*, 12
- Prosthogonimus anatinus*, 14
 - rudolphii*, 14
 - skrjabini*, 14
 - japonicus*, 14
- Schistogonimus rarus*, 14
- Opisthorchis simulans*, 19

TREMATODES—continued:

- Metorchis xanthosomus*, 21
- orientalis*, 21
- Philophthalmus gralli*, 29
- Typhlocelum obovale*, 36
- Tracheophilus sisowi*, 36
- Notocotylus attenuatus*, 37
- egyptiacus*, 37
- Catantropis verrucosa*, 38
- Echinostoma revolutum*, 39
- paraulum*, 40
- Hypoderaum conoideum*, 40
- Echinoparyphium recurvatum*, 41
- Psilochasmus lecithosus*, 45
- Bilharziella polonica*, 51
- yokogawai*, 51
- Strigea gracilis*, 52
- tarda*, 53
- Parastrigea robusta*, 53

CESTODES:

- Raillietina parviuncinata*, 94
- microcotyle*, 94
- anatina*, 94
- Cotugnia fastigata*, 95
- Hymenolepis lanceolata*, 107, 108
- anatina*, 107
- coronula*, 107
- gracilis*, 107
- megalops*, 107
- parvula*, 107
- collaris*, 107
- Echinocotyle rosseteri*, 109
- Fimbriaria fasciolaris*, 110

NEMATODES:

- Porrocaecum crassum*, 134
- Heterakis gallinæ*, 135, 136
- dispar*, 137
- Ascaridia perspicillum*, 137
- lineata*, 137
- Trichostrongylus tenuis*, 181
- Epomidiostomum uncinatum*, 202
- Acuaria (Echinuria) uncinata*, 239
- jugadornata*, 239
- Tropisurus fissispinus*, 240
- gigas*, 241
- (Microtetrameres) inflatus*, 241
- Oxyuris parvovum*, 247
- Hystrichis tricolor*, 254, 255
- Capillaria contorta*, 264, 265

ACANTHOCEPHALA:

- Polymorphus boschadis*, 269
- Filicollis anatis*, 270

GOOSE

TREMATODES:

- Prosthogonimus ovatus*, 13
- Hyptiasmus tumidus*, 35

TREMATODES—continued:

- Notocotylus attenuatus*, 37
- Catantropis verrucosa*, 38
- Paramonostomum alveatum*, 38
- Echinostoma revolutum*, 39
- paraulum*, 40
- Hypoderaum conoideum*, 40
- Strigea tarda*, 53

CESTODES:

- Hymenolepis lanceolata*, 107, 108
- anatina*, 107
- setigera*, 107
- tenuirostris*, 107
- gracilis*, 107
- collaris*, 107
- fasciata*, 107
- Fimbriaria fasciolaris*, 110

NEMATODES:

- Heterakis gallinæ*, 135, 136
- dispar*, 137
- Ascaridia lineata*, 137
- anseris*, 138
- Syngamus trachea*, 161
- Cyathostoma bronchialis*, 163
- Trichostrongylus tenuis*, 181
- Amidostomum nodulosum*, 199, 200
- Epomidiostomum orispinum*, 202
- skrjabini*, 201, 202
- Acuaria (Echinuria) uncinata*, 239
- Capillaria anatis*, 264

PIGEON

TREMATODES:

- Echinostoma columbæ*, 40
- "*Echinostoma*" sp., 40
- Harmostomum commutatum*, 46
- mazzantii*, 46
- "*Distoma columbæ*," 46

CESTODES:

- Aporina delafondi*, 82
- Raillietina crassula*, 94
- clerci*, 94
- nagpurensis*, 94
- columbæ*, 94
- Cotugnia cuneata* var. *tenuis*, 96
- var. *nervosa*, 96
- Houttuynia torquata*, 96

NEMATODES:

- Ascaridia columbæ*, 138
- Ornithostrongylus quadriradiatus*, 189, 190
- Acuaria (Dispharynx) spiralis*, 238
- Tropisurus fissispinus*, 240
- confusus*, 241
- Capillaria columbæ*, 264, 265

GENERAL INDEX

A

- abderus*, *Diloboderus*, 273
abnormalis, *Nematodirus*, 194
Abramis brama, 24, 43
abstrusus, *Ælurostrongylus*, 176
Acanthocephala, 266
Acanthocheilonema, 208
 dracunculoides, 209
 evansi, 209
 gracile, 208
 grassii, 209
 perstans, 205, 208
 reconditum, 209
Acanthogobius, 24
Acanthophorus, 240
 horridus, 240
 tenuis, 240
Acerina, 71
Acheilognathus, 20, 26
Acheilostoma, 170
 paraneator, 170
actinoides, *Thysanosoma*, 89
Acuaria, 237
 hamulosa, 237
 jugadornata, 239
 nasuta, 238
 spiralis, 238
 uncinata, 239
Acuariinae, 237
acuminata, *Limnæa*, 50
acuticaudatum, *Craterostomum*, 151
adersi, *Trichonema* (*Cyclocyclus*), 154
Aedes pseudoscutellaris, 210
 togoi, 210
 variegatus, 210
ægyptiacum, *Trichonema* (*Cylicostomum*), 154
ægyptiacus, *Gastrodiscus*, 61
ægyptiacus, *Notocotylus*, 37
Ælurostrongylus, 176
 abstrusus, 176
æquabilis, *Hymenolepis*, 107
æqualis, *Heterophyes*, 24
aerophilus, *Eucoleus*, 266
affinis, *Trichocephalus*, 261
africana, *Physopsis*, 32, 48, 49
africana, *Schistosoma spindalis* var., 50
africana, *Tænia*, 114
africanus, *Bullinus* [*Physopsis*], 48
africanus, *Mansonioides*, 210
Agamofilaria, 220
 eiseni, 220
 georgiana, 220
 oculi, 220
 palpebralis, 220
 Agamofilaria streptocerca, 221
agilis, *Cyclops*, 107
Aglossa dimidiata, 106
agrestis, *Agriolimax*, 91
Agriolimax agrestis, 91
Agriostomum vryburgi, 165
Akis goryi, 232
 spinosa, 106
Alaria, 54
 alata, 54
 americana, 54
 michiganensis, 54
alata, *Alaria*, 54
alba, *Moniezia*, 83
albidus, *Metorchis*, 21
albimanus, *Anopheles*, 210
alexandrina, *Physa*, 48
alfortensis, *Thelazia*, 246
Alfortia, 149
algeriensis, *Anopheles*, 210
Allodapa brumpti, 139
 differens, 139
Allolobophora, 97
aluconis, *Centrorhynchus*, 271
alveatum, *Paramonostomum*, 38
alveatum, *Trichonema* (*Cylicocercus*), 155
ambiguus, *Passalurus* (*Oxyuris*), 141
americana, *Alaria*, 54
americana, *Periplaneta*, 275
americanum, *Diphylobothrium*, 68
americanus, *Necator*, 166
americanus, *Tropisurus*, 241
Amidostomidae, 199
Amidostomum, 200
 nodulosum, 199, 200
Amœbotænia, 97
 sphenoides, 97
Amphilinoinei, 63
Amphimerus, 19
Ampullaria luteostoma, 28, 31
amucronatus, *Globocephalus*, 168
anastrophus, *Balanorchis*, 58, 59
anatina, *Hymenolepis*, 107
anatina, *Raillietina*, 94
anatinum, *Epomidiostomum*, 202
anatinus, *Prosthogonimus*, 14
anatis, *Capillaria*, 264
anatis, *Filicollis*, 270
Ancylostoma, 164
 braziliense, 164
 caninum, 164
 ceylanicum, 164
 duodenale, 164
Ancylostomidae, 163

- Ancylostominae*, 164
Angiostrongylus, 171, 177
 vasorum, 177
Anguillulidæ, 128
Anisakinae, 134
anisocotylea, *Paramphistomum*, 56
Anisolabis annulipes, 106
annamense, *Harmostomum*, 276
annulata, *Capillaria*, 264
annulipes, *Anisolabis*, 106
Anoa depressicornis, 60
Anomotænia, 77
Anopheles albimanus, 210
 algeriensis, 210
 bifurcatus, 207
 costalis, 210
 maculipennis, 207, 209
 rossii, 210
 sinensis, 210
Anoplocephala, 79
 magna, 80
 mamillana, 80, 81
 minima, 81
 perfoliata, 80
 plicata, 80
Anoplocephalidæ, 79
Anoplocephaloides, 81
anseris, *Ascaridia*, 138
anseris, *Strongylus*, 200
antarctica, *Tænia*, 115
Anthuris, 237
antiguensis, *Planorbis*, 48
apapillocephala, *Filaria*, 220
Aphodius castaneus, 229
 coloradensis, 234
 femoralis, 234
 fimetarius, 234
 granarius, 234
 hæmorrhoidalis, 235
 rufus, 229
 vittatus, 234
apiostomum, *Æsophagostomum*, 158, 159
apivorus, *Pernis*, 19
Aporina, 81
 delafondi, 82
appendiculatum, *Prohemistomum*, 53
apri, *Metastrongylus*, 171, 172
apri, *Trichocephalus*, 258
aretica, *Spirocerca*, 232
arcuata, *Lachnosterna*, 273
arcuatum, *Cyclocœlum*, 35
arcuatum, *Lepoderma*, 12
Arduenna, 228
 dentata, 229
 strongylina, 228
Arduenninae, 227
arietis, *Platynosomum*, 16
Arion, 15
armatum, *Stamnosoma*, 26
armillata, *Onchocerca*, 214
arnfieldi, *Dictyocaulus*, 174
arquatus, *Numenius*, 14
Ascaridæ, 128
Ascaridia, 137
 anseris, 138
 brasilensis, 137
 columbæ, 138
Ascaridia compar, 137
 compressa, 138
 granulosa, 138
 hamia, 137
 inflexa, 137
 lineata, 137
 maculosa, 138
 perspicillum, 137
 styplocerca, 138
Ascarinae, 129
Ascaris, 129
 equorum, 131
 lumbricoides, 129
 maritima, 132
 megaloccephala, 131
 ovis, 129
 suilla, 129
 suis, 129
 texana, 132
 vitulorum, 131
Ascaroidea, 123, 128
Ascocotyle, 26
 italica, 26
 minuta, 26
asiatica, *Raillietina*, 92
asini, *Strongylus* (*Delafondia*), 148, 149, 150
Asopia farinalis, 106
asperum, *Æsophagostomum*, 158
Aspidogastroidæ, 6
Aspius, 54
 aspius, 43
Astacus dauricus, 28
 japonicus, 28
 similis, 28
astacus, *Potamobius*, 269
asymmetricum, *Trichonema* (*Cylicotetrapedon*), 155
Ateuchus sacer, 230, 232, 235
Atractidæ, 128
attenuatus, *Notocotylus*, 37
auquieri, *Microfilaria*, 221
aurata, *Cetonia*, 273
auratus, *Carassius*, 20, 26
auriculatum, *Trichonema* (*Cylicocycclus*), 152, 154
austeni, *Culicoides*, 209
Avitellina, 83, 84
 centripunctata, 84, 85, 86
 chalmersi, 86
 goughi, 86
 laciniosa, 86
 lahorea, 86
 sudanea, 86
Avitellininae, 84
axei, *Trichostrongylus*, 181

B

- bailleti*, *Dithyridium*, 79
balaniceps, *Tænia*, 115
Balanorchis, 58
 anastrophus, 58, 59
baneroffi, *Wuchereria*, 204, 210
barbatum, *Trichonema*, 154
bauchei, *Hymenolepis*, 106
baxteri, *Sparganum*, 72, 73
bedeli, *Onthophagus*, 230, 235

- Belascaris*, 133
 cati, 133
 marginata, 133
benedeni, Moniezia, 83
beramporia, Heterakis, 136
bernardi, Setaria, 218
Bertiella, 81
 satyri, 81
 studeri, 81
bicornis, Trapa, 34
bicoronatum, Trichonema (Cyclicodontophorus), 155
bicuspidatus, Cyclops, 223
bidentatum, Trichonema (Cyclicotetrapedon), 155
bifurcatus, Anopheles, 207
Bilharzia, 46
Bilharziella, 51
 polonica, 51
 yokogawai, 51
birmanica, Raillietina, 94
björkna, Blicca, 24, 43
Blanfordia formosana, 49
 japonica, 49
 nosophora, 26
Blaps, 235
 mucronata, 275
Blattella germanica, 235
Blicca, 54
 björkna, 24, 43
blini, Filaria, 215
boissyi, Planorbis, 48
bomfordi, Schistosoma, 49, 50
Bos caffer, 216
 indicus, 17
 sinicus, 49
boschadis, Polymorphus, 269
Bothriocephalidea, 63, 66
Bourgelatia, 157
 diducta, 157
bovis, Capillaria, 263
bovis, Cysticercus, 113
bovis, Onchocerca, 214
bovis, Schistosoma, 49, 50
brachysoma, Tænia, 115
brama, Abramis, 24, 43
brasiliensis, Ascaridia, 137
brauni, Diplogonoporus, 74
brauni, Prosthogonimus, 14
brauni, Tænia, 115, 116
Braunia, 74
 jassyiensis, 75
braziliense, Ancylostoma, 164
bremneri, Tænia, 114
brevicapsulatum, Trichonema (Cyclicobrachytus), 155
brevicauda, Triodontophorus, 151
brevicaudatus, Cyclops, 107
brevipes, Capillaria, 262
brevispiculum, Heterakis, 136
brevispinosus, Cyclops, 70
brevivaginatus, Metastrongylus, 173
bronchialis, Cyathostoma, 163
brumpti, Oesophagostomum, 158, 159
brumpti, Subulura (Allodapa), 139
buencaminoi, Dipylidium, 101
bulimoides, Cleopatra, 61
Bullinus africanus, 48
 contortus, 48
 dybowskii, 48, 56
 forskali, 56
bullosa, Ostertagia, 188
Bunodera, 34
 linearis, 34
Bunoderidæ, 34
Bunostomum, 168
 phlebotomum, 169
 trigonocephalum, 168
bursa, 122, 147
buskii, Fasciolopsis, 32, 33
Bythia, 18
 fuchsiana, 20
 longicornis, 20
- C
- Caccobius schreberi*, 235
cæcutiens, Onchocerca, 212
caffer, Bos, 216
cahirensis, Rictularia, 249
Cairina moschata, 247
calcitrans, Stomoxys, 108, 225
calicatum, Trichonema, 154
callipæda, Thelazia, 246
calopus, Stegomyia, 221
Cambaroides dauricus, 28
 similis, 28
cameli, Trichuris, 261
campanula, Trichuris, 260
campanulatus, Echinorhynchus, 274
canadense-griseum, Stizostedion, 71
candida, Candona, 107
Candona candida, 107
 rostrata, 107
caninum, Ancylostoma, 164
caninum, Dipylidium, 99, 101
caninus, Centrocestus cuspidatus, 26
caninus, Opisthorchis, 19
Canis latrans, 19
 lestes, 25
canis, Ctenocephalus, 99
canis, Echinorhynchus, 275
canis, Oncicola, 273
canis, Strongyloides, 146
canis, Toxocara, 133
canis, Trichodectes, 99
canis bronchialis, Strongylus, 177
cantaniana, Hymenolepis, 106
Capillaria, 261
 anatidis, 264
 annulata, 264
 bovis, 263
 brevipes, 262
 caudinflata, 264
 collaris, 264
 columbæ, 264, 265
 contorta, 264, 265
 dubia, 264
 felis-cati, 263
 gallina, 264
 linearis, 263
 longicollis, 264
 longipes, 263
 meleagris-gallopavo, 264

- Capillaria plica*, 263
 retusa, 264
capillaris, *Muellerius*, 175, 176
capitatus, *Gyaloccephalus*, 156
capræ, *Filaria*, 220
capricola, *Trichostrongylus*, 180
Carassius, 54
 auratus, 20, 26
carioca, *Hymenolepis* (*Weinlandia*), 106, 108
Carmyerius, 60
 gregarius, 61
 spatiosus, 61
carthusianella, *Helix*, 93
castaneus, *Aphodius*, 229
Catatropis, 38
 verrucosa, 37, 38
cati, *Belascaris*, 133
catinatum, *Trichonema* (*Cylicocercus*), 155
cattoi, *Schistosoma*, 49
catulinus, *Macracanthorhynchus*, 273
caucasica, *Physaloptera*, 242, 243
caudinflata, *Capillaria*, 264
caudispina, *Dipetalonema*, 208
cellulosæ, *Cysticercus*, 112
centimetralis, *Planorbis*, 48
centripunctata, *Avitellina*, 84, 85, 86
Centrocestus, 26
 cuspidatus caninus, 26
Centrorhynchus, 271
 aluconis, 271
 erraticus, 271
cephalus, *Mugil*, 23, 24
Ceratophyllus fasciatus, 106
Cercaria, 8, 10
Cercaria echinata, 39
Cercocystis, 77
cerebralis, *Cœnurus*, 115, 116
cervi, *Paramphistomum*, 56
cervicalis, *Onchocerca*, 213
cervina, *Filaria*, 216
cesticillus, *Raillietina*, 93, 94
cesticillus, *Skrjabinia*, 94
Cestodes, 62
Cestoidea, 62
Cetonia aurata, 273
ceylanicum, *Ancylostoma*, 164
ceylonensis, *Fiscoederius*, 60
Chabertia ovina, 159
chalmersi, *Avitellina*, 86
Characostomum, 167
Cheilospirura, 237
 hamulosa, 237
Cheiracanthus, 249
 robustus, 250
 siamensis, 250
cheopis, *Xenopsylla*, 106
Chlamydonema, 242
 felineum, 243
Choanotænia, 97
 infundibulum, 97, 98
Chœrostrongylus, 173
 pudendotectus, 172, 173
Chrysops, 205, 219
 dimidiata, 219
 silacea, 219
chyzeri, *Joyeuxia*, 101, 102
cincinnati, *Spiroptera*, 213
 cinereus, *Limax*, 91
cingulatus, *Pyradus*, 26
circumcincta, *Ostertagia*, 186
Cladorchis, 59
 giganteus, 59
Cleopatra bulimoides, 61
 cyclostomoides, 61
clerci, *Raillietina*, 94
Clonorchis, 19
 endemicus, 20
 sinensis, 20
cobboldii, *Fiscoederius*, 60
Cobus, 59
cœlomaticum, *Eurytrema*, 17
cœnosus, *Planorbis*, 33
Cœnurus, 111
 cerebralis, 115, 116
cœnurus, *Tænia*, 115
cohnii, *Raillietina*, 94
collaris, *Capillaria*, 264
collaris, *Hymenolepis* (*Weinlandia*), 107
collinsii, *Pesudodiscus*, 58
Collyriclum, 28
 faba, 29
coloradensis, *Aphodius*, 234
colubrifomis, *Trichostrongylus*, 180
columbæ, *Ascaridia*, 138
columbæ, *Capillaria*, 264, 265
columbæ, *Distoma*, 46
columbæ, *Echinostoma*, 40
columbæ, *Raillietina* (*Skrjabinia*), 94
columbianum, *Æsophagostomum*, 157, 158, 159
commutatum, *Harmostomum*, 45, 46
compactum, *Dipylidium*, 101
compactus, *Stephanopharynx*, 59
compar, *Ascaridia*, 137
compar, *Oxyuris*, 141
complanatus, *Planorbis*, 15
complexus, *Parametorchis*, 21
compressa, *Ascaridia*, 138
compressus, *Gastrothylax*, 60
confusa, *Tænia*, 114
confusum, *Gongylonema*, 233
confusus, *Tropisurus*, 241
conjunctivæ, *Filaria*, 220
connorfilii, *Globocephalus*, 167
conoideum, *Hypoderaum*, 40
continuus, *Heterophyes*, 24
contorta, *Capillaria*, 264, 265
contortus, *Bullinus*, 48
contortus, *Hæmonchus*, 190, 191, 192
Cooperia, 182
 curticei, 182, 183
 oncophora, 183
 pectinata, 182, 183
 punctata, 183
Copris hispana, 232
coracidium, 70
cordatum, *Diphyllbothrium*, 68, 71
cordatum, *Pharyngostomum*, 55
cordicola, *Filaria*, 220
Cordophilus sagitta, 211
Coregonus, 71
corneus, *Planorbis*, 40, 48
coronatum, *Trichonema* (*Cylicostomum*), 154
coronatus, *Cyclops*, 223

- coronula, *Hymenolepis* (Weinlandia), 107
Corynosoma strumosum, 271
costalis, *Anopheles*, 210
Cotugnia, 95
 cuneata, 96
 cuneata var. *nervosa*, 96
 cuneata var. *tenuis*, 96
 digonopora, 95
 fastigata, 95
Cotylophallus, 24
Cotylophoron, 57
 cotylophorum, 57
 indicum, 57
cotylophorum, *Cotylophoron*, 57
crassicauda, *Trichosomoides*, 255
crassicolis, *Tænia*, 115
Crassisoma, 167
crassula, *Raillietina*, 94
crassum, *Dipylidium*, 101
crassum, *Porrocaecum*, 134
crassum, *Schistosoma*, 49
Craterostomum, 151
 acuticaudatum, 151
 mucronatum, 151
 tenuicauda, 151
crenatum, *Gongylonema*, 235
crenatus, *Trichocephalus*, 258
cristata, *Testifrons*, 44
cristatus, *Physocephalus*, 230
cristatus, *Sus*, 44, 229
crumenifer, *Gastrothylax*, 60
Cryptocotyle, 26
 lingua, 26
Cryptocystis, 77
Ctenocephalus canis, 99
Ctenopharyngodon idellus, 20
Culex fatigans, 207, 210
 penicillaris, 207
 pipiens, 207, 210
 sitiens, 210
 vexans, 207
Culicoides, 205
 austeni, 209
 grahami, 209
cuneata, *Cotugnia*, 96
cuneatus, *Prosthogonimus*, 13, 14
curticei, *Cooperia*, 182, 183
curvula, *Oxyuris*, 141
Cyathostoma, 163
 bronchialis, 163
Cyelas, 41
Cyclocecidæ, 34
Cycloccelum, 35
 arcuatum, 35
 mutabile, 35
Cyclocypris, 107
 globosa, 109
Cyclophyllideæ, 75
Cyclops agilis, 107
 bicuspidatus, 223
 brevicaudatus, 107
 brevispinosus, 70
 coronatus, 223
 leuckarti, 72
 prasinus, 70
 quadricornis, 223
 strenuus, 70
Cyclops viridis, 107
cyclostomoides, *Cleopatra*, 61
cygni, *Hystrix*, 255
Cylichnostomum, 152
Cylicobrachytus, 155
Cylicocercus, 155
Cylicocycylus, 154
Cylicodontophorus, 155
Cylicospirura, 232
 subæqualis, 233
Cylicostephanus, 154
Cylicostomum, 152, 154
Cylicotetrapedon, 155
Cylicotoichus, 155
Cypria ophthalmica, 107, 109
Cyprinus, 26
Cypris, 107
 ovum, 107
cysticeroid, 76, 77
Cysticerus, 76
 bovis, 113
 cellulosæ, 112
 elongatus, 79
 fasciolaris, 116
 ovis, 116
 pisiformis, 116
 tarandi, 116
 tenuicollis, 116

D

- dajii*, *Eurytrema*, 17, 18
damnosum, *Simulium*, 212
danubiense, *Pseudamphistomum*, 22
Daphnia pulex, 239, 241
dauricus, *Astacus* (*Cambaroides*), 28
Davainea, 90
 proglottina, 77, 90, 91
Davaineidæ, 90
Davainoides, 93
 vigintivasus, 95
dealbatus, *Erinaceus*, 232
decipiens, *Diphyllbothrium*, 68
dehaani, *Potamon* (*Geothelphusa*), 28
dehaani, *Sesarma*, 28
delafondi, *Aporina*, 82
Delafondia, 150
demarquayi, *Filaria*, 219
demerariensis, *Raillietina*, 92
deminutus, *Ternidens*, 159
dendriticum, *Dicroccelum*, 15
dentata, *Arduenna*, 229
dentatum, *Cesophagostomum*, 168
dentatus, *Stephanurus*, 160
denticulata, *Moniezia*, 83
depressicornis, *Anoa*, 60
depressiusculus, *Trichocephalus*, 260
Dermofilaria irritans, 226
Diaptomus gracilis, 70
 oregonensis, 70
 spinosus, 107
 vulgaris, 110
Dibothriocephalus, 67
Dicroccellidæ, 14
Dicroccelum, 15

Dicrocoelium dendriticum, 15
 hospes, 15
 lanceatum, 15
 lanceolatum, 15
 macrostomum, 16

Dictyocaulus, 173
 arnfieldi, 174
 filaria, 173, 177
 viviparus, 174

diducta, Bourgelatia, 157
differens, *Subulura* (*Allodapa*), 139

diffusum, *Dipylidium*, 101

Digenea, 6

digitata, *Setaria*, 217

digitatus, *Mecistocirrus*, 197, 198

digonopora, *Cotugnia*, 95

Dilepididae, 96

Diloboderus abderus, 273

dimidiata, *Aglossa*, 106

dimidiata, *Chrysops*, 219

diminuta, *Hymenolepis*, 105

Diotophyme, 252

renalis, 253

Diotophymidae, 252

Diotophymoidea, 252

Dipetalonema, 208

caudispina, 208

Diphyllobothriidae, 66

Diphyllobothriidae, 66

Diphyllobothrium, 67

americanum, 68

cordatum, 68, 71

decipiens, 68

fuscum, 68

latum, 67, 68, 69, 70

mansoni, 68, 72

parvum, 71

raillieti, 68, 72

ranarum, 68

reptans, 68

Diplogonoporus, 74

brauni, 74

grandis, 74

Diplopylidium, 100

nöllerii, 101

quiquecoronatum, 101

trinchessii, 100, 101, 102

Dipylidium, 77, 98

buencaminoi, 101

caninum, 99, 101

compactum, 101

crassum, 101

diffusum, 101

gracile, 101

halli, 101

longulum, 101

oerleyi, 101

rossicum, 101

sexcoronatum, 100, 101

walkerii, 101

Dirofilaria, 206

immitis, 206

magalhãesii, 207

repens, 207

discolor, *Trichuris*, 261

dispar, *Heterakis*, 137

dispar, *Heterophyes*, 24

dispar, *Syngamus*, 163

dispar, *Trichocephalus*, 258

Dispharagus, 237

Dispharynx, 237

nasuta, 238

spiralis, 238

Distoma columbæ, 46

Dithyridium, 76, 78

bailleti, 79

lacertæ, 78

diurna, *Microfilaria*, 219

doloresi, *Gnathostoma*, 252

domestica, *Musca*, 98, 225

donicum, *Rossicotrema*, 24

douei, *Geotrupes*, 230, 232, 235

dracunculoides, *Acanthocheilonema*, 209

Dracunculus medinensis, 222

Drepanidotænia, 108

Dreysensia polymorpha, 18

dromedarii, *Nematodirus*, 196

dubia, *Capillaria*, 264

duodenale, *Ancylostoma*, 164

dybowskii, *Bullinus*, 48, 56

E

echinata, *Cercaria*, 39

echinatum, *Echinostoma*, 39

echinobothrida, *Raillietina*, 92, 93, 94

Echinobothriidea, 63

Echinocephalus, 251

Echinochasmus, 43

perfoliatus, 43

perfoliatus japonicus, 43

Echinococcus, 117

granulosus, 117

Echinocotyle, 109

rosseteri, 109

Echinopardalis, 274

pardalis, 274

Echinoparyphium, 41

recurvatum, 41

echinophyllus, *Trichocephalus*, 261

Echinorhynchidae, 269

Echinorhynchus campanulatus, 274

canis, 275

filicollis, 270

gigas, 272

grassii, 275

hominis, 275

minutus, 269

ovatus, 274

Echinostoma, 39, 40

columbæ, 40

echinatum, 39

ilocanum, 40

paraulum, 40

revolutum, 39

Echinostomatidae, 38

Echinuria, 237, 238

jugadornata, 239

uncinata, 239

edentatus, *Strongylus* (*Alfortia*), 148, 149, 150

eiseni, *Agamofilaria*, 220

Elæophora poeli, 215

Electris potamophilia, 55

Eliocharis tuberosa, 34

elongatum, *Trichonema* (*Cylicocyclus*), 154
 elongatus, *Cysticercus*, 79
 elongatus, *Fischoederius*, 60
 elongatus, *Metastrongylus*, 172
 endemicus, *Clonorchis*, 20
Enterobius, 142
 vermicularis, 142
Episthmium, 43
 oscari, 44
Epomidiostomum, 201
 anatinum, 202
 orispinum, 202
 skrjabini, 201, 202
 uncinatum, 202
equi, *Gyalocephalus*, 156
equi, *Oxyuris*, 141
equina, *Setaria*, 216
equinus, *Strongylus*, 148, 149
equorum, *Ascaris*, 131
Erinaceus dealbatus, 232
Eriocheir japonicus, 28
 sinensis, 28
erraticus, *Centrorhynchus*, 271
erythrophthalmus, *Scardinius*, 24
Esox lucius, 43, 71
Eucoleus, 266
 aerophilus, 266
Euparyphium, 41
 jassyense, 42
 malayanum, 41, 42
 sufrartyfex, 42
 suinum, 42
euproctus, *Trichonema* (*Cylicodontophorus*), 155
Eurytrema, 16
 coelomaticum, 17
 dajii, 17, 18
 ovis, 17, 18
 pancreaticum, 17, 18
 parvum, 17
 rebelle, 276
Eustrongylides, 252, 254
 mergorum, 241
Eustrongylus gigas, 253
evansi, *Acanthocheilonema*, 209
exigua, *Hymenolepis*, 106
exilis, *Hymenolepis*, 106
expansa, *Moniezia*, 82
explanatum, *Paramphistomum*, 57
extenuatus, *Trichostrongylus*, 178, 179
extraocularis, *Filaria* [*Loa*], 219
exustus, *Planorbis*, 50

F

faba, *Collyriclum*, 29
falculatus, *Trichostrongylus*, 180
farinalis, *Asopia*, 106
fasciata, *Hymenolepis*, 107
fasciata, *Onchocerca*, 214
fasciata, *Stegomyia*, 207
fasciatus, *Ceratophyllus*, 106
fasciatus, *Lynx*, 25
Fasciola, 11, 30
 gigantica, 31
 hepatica, 9, 30, 31
 magna, 32

fasciolaris, *Cysticercus*, 116
fasciolaris, *Fimbriaria*, 110
Fascioletta ilocana, 40
Fasciolidæ, 30
Fascioloidæ, 6
Fascioloides, 32
Fascioloinæ, 6
Fasciolopsis, 32, 33
 buskii, 32, 33
 fülleborni, 33
 goddardi, 33
 rathouisi, 33
 spinifera, 33
fastigata, *Cotugnia*, 95
fastosum, *Platynosomum*, 16
fatigans, *Culex*, 207, 210
fausti, *Katayama*, 49
fedtschenkowi, *Hymenolepis*, 106
felineum, *Chlamydonema*, 243
felineus, *Opisthorchis*, 18, 19
felineus, *Spirocerca*, 233
Felis minuta, 16
felis-cati, *Capillaria*, 263
femoralis, *Aphodius*, 234
ferrugineum, *Tribolium*, 106
Filaria, 205
 apapillocephala, 220
 blini, 215
 capræ, 220
 cervina, 216
 conjunctivæ, 220
 cordicola, 220
 demarquay, 219
 extraocularis, 219
 hæmophila, 215
 hæmorrhagica, 205
 inermis, 220
 juncea, 219
 labialis, 233
 malayi, 221
 martis, 205
 ochmanni, 207
 ozzardi, 219, 221
 pulicis, 240
 sanguinis hominis diurna, 204
 sanguinis hominis nocturna, 204
Filaria sp., 221
 spirovoluta, 220
 taniguchii, 219
filaria, *Dictyocaulus*, 173, 177
Filariidæ, 203
Filarioidea, 202
Filicollis, 269
 anatis, 270
filicollis, *Echinorhynchus*, 270
filicollis, *Nematodirus*, 194
Fimbriaria, 109
 fasciolaris, 110
finetarius, *Aphodius*, 234
fischoederi, *Fischoederius*, 60
Fischoederius, 60
 ceylonensis, 60
 cobboldii, 60
 elongatus, 60
 fischoederi, 60
 siamensis, 60
fissispina, *Tropidocerca*, 240

fissispinus, *Tropisurus*, 240
 Flatworms, 3
flavopunctata, *Tænia*, 105
flavus, *Limax*, 91
 Flukes, 5
fontinale, *Pisidium*, 15
fontinalis, *Physa*, 31
fordii, *Mecistocirrus*, 198
formosana, *Katayama* [*Blanfordia*], 49
formosana, *Raillietina*, 93
formosanum, *Stammosoma*, 26
formosus, *Plagiorhynchus*, 271
forskali, *Bullinus*, 56
fraterna, *Hymenolepis nana*, 104
frontalis, *Palonia*, 60
fuchsiana, *Bythinia*, 20
Fuellebornius, 222
Fuhrmannetta, 91
fülleborni, *Fasciolopsis*, 33
fulvus, *Oniticellus*, 235
furcatus, *Nematodirus*, 196
furcifer, *Prosthogonimus*, 276
fuscopennatus, *Taniorhynchus*, 209
fuseum, *Diphylobothrium*, 68

G

gaigeri, *Tænia* (*Multiceps*), 115, 116
Gaigeria, 169
 pachyscelis, 169
gallina, *Capillaria*, 264
gallinæ, *Heterakis*, 135, 136
gallinarum, *Hartertia*, 227
gallinarum, *Southwellia*, 98
gallineis, *Tropisurus*, 241
Gammarus pulex, 107, 241, 269
Gasterostomata, 6
Gastrodiscoides, 62
Gastrodiscus, 61
 egyptiacus, 61
 hominis, 62
 minor, 61
 secundus, 61
Gastrothylax, 59
 compressus, 60
 crumenifer, 60
Gatesius, 73
gemina, *Physaloptera*, 244
georgiana, *Agamofilaria*, 220
Geothelphusa dehaani, 28
Geotrupes douei, 230, 232, 235
 sylvaticus, 98
germanica, *Blattella*, 235
giardi, *Helicometra*, 89
gibsoni, *Mecistocirrus*, 198
gibsoni, *Onchocerca*, 213
giganteus, *Cladorchis*, 59
gigantica, *Fasciola*, 31
Gigantorhynchidæ, 271
Gigantorhynchus gigas, 272
gigas, *Echinorhynchus*, 272
gigas, *Eustrongylus*, 253
gigas, *Gigantorhynchus*, 272
gigas, *Tropisurus*, 241
globipunctata, *Stilesia*, 88
Globocephalus, 167
 amucronatus, 168
 connorfilii, 167

Globocephalus longemucronatus, 167
 samoensis, 167
 urosubulatus, 167
globosa, *Cyclocypris*, 109
globosa, *Physopsis*, 48
globulosa, *Trichuris*, 261
glomeratus, *Multiceps*, 116
Gnathostoma, 249, 251
 doloresi, 252
 hispidum, 252
 spinigerum, 250
Gnathostomidæ, 249
Gnathostominae, 249
goddardi, *Fasciolopsis*, 33
goldi, *Trichonema* (*Cylicocercus*), 155
Gongylonema, 233
 confusum, 233
 crenatum, 235
 hominis, 233
 ingluvicola, 236
 monnigi, 235, 236
 pulchrum, 233, 235
 ransomi, 233
 subtile, 233
 verrucosum, 234, 235
goryi, *Akis*, 232
gotoi, *Paramphistomum*, 56
goughi, *Avitellina*, 86
gracile, *Acanthocheilonema*, 208
gracile, *Dipylidium*, 101
gracilis, *Diaptomus*, 70
gracilis, *Hymenolepis* (*Weinlandia*), 107, 108, 109
gracilis, *Strigea*, 52
grahami, *Calicoides*, 209
gralli, *Philophthalmus*, 29
granarius, *Aphodius*, 234
grandis, *Diplogonoporus*, 74
granella, *Tinea*, 106
granulosa, *Ascaridia*, 138
granulosus, *Echinococcus*, 117
grassii, *Acanthocheilonema*, 209
grassii, *Echinorhynchus*, 275
gregarius, *Carmyerius*, 61
grobbeni, *Raillietina*, 94
Gromphas lacordairei, 273
guadeloupensis, *Planorbis*, 48
Guinea-worm, 222
gularis, *Paralipsa*, 106
gulosa, *Thelazia*, 246
gutturosa, *Onchocerca*, 214
guyanensis, *Microfilaria*, 221
Gyalocephalus, 156
 capitatus, 156
 equi, 156
Gymnopleurus mopsus, 235
 sturmi, 230, 232, 235

H

Habronema, 223
 megastoma, 225
 microstoma, 224
 muscæ, 223, 224
hæmatobium, *Schistosoma*, 47, 48, 50
Hæmonchus, 191
 contortus, 190, 191, 192

- Hæmonchus longistipes*, 193
 lunatus, 193
 similis, 192
hæmophila, *Filaria*, 215
hæmorrhagica, *Filaria*, 205
hæmorrhoidalis, *Aphodius*, 235
Hæmostrongylus, 171, 177
halli, *Dipylidium*, 101
hamia, *Ascaridia*, 137
hamulosa, *Acuaria*, 237
Harmostomidae, 45
Harmostomum, 45
 annamense, 276
 commutatatum, 45, 46
 mazzantii, 46
Hartertia, 226
 gallinarum, 227
hecate, *Onthophagus*, 229, 234
Helictometra giardi, 89
Heligmosominae, 198
Helix, 45
 carthusianella, 93
 maculosa, 93
helvetianus, *Nematodirus*, 196
Hemiculter kneri, 20
hepatica, *Fasciola*, 9, 30, 31
hepatica, *Hepaticola*, 265
hepatica, *Stilesia*, 87
Hepaticola, 265
 hepatica, 265
Herpobdella octoculata, 107
Heterakidae, 128, 135
Heterakinae, 135
Heterakis, 135
 beramporia, 136
 brevispiculum, 136
 dispar, 137
 gallinae, 135, 136
 isolonche, 136
 papillosa, 136
 putaustralis, 136
 vesicularis, 136
Heterodera radiculicola, 141
Heterophyes, 23
 æqualis, 24
 continuus, 24
 dispar, 24
 heterophyes, 23
 katsuradai, 24
 limatus, 24
 nocens, 23
 persicus, 24
Heterophyidae, 22
Hexastichorchis pintneri, 86
hirudinaceus, *Macracanthorhynchus*, 272
hispana, *Copris*, 232
hispidum, *Gnathostoma*, 252
Histioccephalus, 227
 laticaudatus, 227
Hodotermes pretoriensis, 227
holomyarian, 123
Holostomidae, 52
Homalogaster, 62
 paloniæ, 62
 philippinensis, 62
 poirieri, 62
hominis, *Echinorhynchus*, 275
 hominis, *Gastrodiscus*, 62
 hominis, *Gongylonema*, 233
 hominis, *Tænia*, 114
 hominis, *Trichocephalus*, 258
hongkongensis, *Melania*, 20
Hookworms, 163
horridus, *Acanthophorus*, 240
hospes, *Dicrocoelium*, 15
Houttuynia, 96
 torquata, 96
humilis, *Limnæa*, 31
hupensis, *Oncamelania*, 49
hybridum, *Trichonema*, 154
hydatid, 117
hydatigena, *Tænia*, 114, 115, 116
Hydatigera, 111
Hymenolepididae, 77, 102
Hymenolepis, 77, 102
 æquabilis, 107
 anatina, 107
 bauchei, 106
 cantaniana, 106
 carioca, 106, 108
 collaris, 107
 coronula, 107
 diminuta, 105
 exigua, 106
 exilis, 106
 fasciata, 107
 fedtschenkowi, 106
 gracilis, 107, 108, 109
 inermis, 106
 lanceolata, 107, 108
 megalops, 107
 meleagris, 106
 musculosa, 106, 108
 nana, 103, 104, 105
 nana, var. *fraterna*, 104
 parvula, 107
 pullæ, 106
 rustica, 106
 setigera, 107
 tenuirostris, 107
 tichodroma, 106
 villosa, 106
Hyoststrongylus rubidus, 183
Hypoderaum, 40
 conoideum, 40
Hypothalmichthys nobilis, 20
Hyptiasmus, 35
 tumidus, 35
Hystrichis, 252, 254
 cygni, 255
 pachicephalus, 255
 tricolor, 255

I

- ichikawai*, *Paramphistomum*, 56
idellus, *Ctenopharyngodon*, 20
Idus idus, 43, 254
 melanotus, 18
ihlei, *Trichonema*, 155
ijimai, *Paramphistomum*, 57
ilocana, *Fascioletta*, 40
ilocanum, *Echinostoma*, 40
immitis, *Dirofilaria*, 206
imparidentatum, *Poteriostomum*, 156

incognita, *Oxyuris*, 141
 incognitum, *Schistosoma*, 51
 indica, *Onchocerca*, 214
 indicum, *Cotylophoron*, 57
 indicum, *Schistosoma*, 50
 indicus, *Bos*, 17
 indurium, *Prohemistomum*, 54
 inermis, *Filaria*, 220
 inermis, *Hymenolepis*, 106
 infantis, *Tænia*, 114
 inflatus, *Tropisurus* (*Microtetrameres*), 241
 inflexa, *Ascaridia*, 137
 infundibulum, *Choanotænia*, 97, 98
 ingluvicola, *Gongylonema*, 236
 innesi, *Isidora*, 48
 insigne, *Trichonema* (*Cylicocycylus*), 154
 instabilis, *Trichostrongylus*, 180
 intercalandus, *Prosthogonimus*, 13
 intermedius, *Triodontophorus*, 151
 irritans, *Dermofilaria*, 226
 irritans, *Pulex*, 99
 irroratus, *Onitis*, 235
 Isidora innesi, 48
 tropica, 31, 48
 isolonche, *Heterakis*, 136
 italica, *Ascocotyle*, 26
 iturbei, *Pseudotephusa*, 28

J

japonica, *Blanfordia*, 49
 japonica, *Limnæa*, 31
 japonicum, *Schistosoma*, 49, 50
 japonicus, *Astacus*, 28
 japonicus, *Echinochasmus perfoliatus*, 43
 japonicus, *Eriocheir*, 28
 japonicus, *Mugil*, 23
 japonicus, *Prosthogonimus*, 14
 jassyense, *Euparyphium*, 42
 jassyensis, *Braunia*, 75
 Joyeuxia, 100
 chyzeri, 101, 102
 pasqualei, 101
 jugadornata, *Acuaria* (*Echinuria*), 239
 juncea, *Filaria*, 219

K

Katayama fausti, 49
 formosana, 49
 nosophora, 26, 49
 Kathlaniidæ, 128, 139
 katsuradai, *Heterophyes*, 24
 kellicotti, *Paragonimus*, 28
 kingi, *Syngamus*, 163
 kneri, *Hemiculter*, 20
 krabbei, *Tænia*, 115, 116

L

labialis, *Filaria*, 233
 labiato-papillosa, *Setaria*, 216
 labiatum, *Trichonema* (*Cylicostomum*), 154
 labratum, *Trichonema* (*Cylicostomum*), 154
 lacerta, *Dithyridium*, 78
 Lachnosterna arcuata, 273
 laciniosa, *Avitellina*, 86
 lacordairei, *Gromphas*, 273

lacrymalis, *Thelazia*, 246
 lævis, *Porcellio*, 238
 Lagochilascaris, 133
 minor, 134
 lagopus, *Vulpes*, 232
 lahorea, *Avitellina*, 86
 lanceatum, *Dicrocoelium*, 15
 lanceolata, *Hymenolepis*, 107, 108
 lanceolatum, *Dicrocoelium*, 15
 Laphyctes, 248
 largillierti, *Planorbis* (*Segmentina*), 33
 laryngeus, *Syngamus*, 162
 laticaudatus, *Histiocephalus*, 227
 latrans, *Canis*, 19
 latum, *Diphylobothrium*, 67, 68, 69, 70
 lecitithosus, *Psilochasmus*, 45
 leesei, *Thelazia*, 247
 leonina, *Toxascaris*, 133
 Lepoderma, 11
 arcuatum, 12
 massino, 12
 potanini, 12
 Lepodermatidæ, 11
 leporis, *Nematodirus*, 196
 leptostomum, *Trichonema* (*Cylicocycylus*), 154
 lestes, *Canis*, 25
 Leuciscus, 26
 rutilus, 18, 21
 leuckarti, *Cyclops*, 72
 Leucogobio, 20
 Leucophaea surinamensis, 248
 lewisii, *Microfilaria*, 221
 Libellula quadrimaculata, 13
 libertina, *Melania*, 20
 lienalis, *Onchocerca*, 214
 Ligula, 74
 ranarum, 68
 Ligulinæ, 75
 limatus, *Heterophyes*, 24
 Limax, 15
 cinereus, 91
 flavus, 91
 variegatus, 91
 limbata, *Toxascaris*, 133
 Limnæa, 53
 acuminata, 50
 humilis, 31
 japonica, 31
 limosa, 40, 41
 natalensis, 31, 32, 48
 oahuensis, 31
 palustris, 41
 peregra, 40
 pervia, 31
 rubella, 31
 stagnalis, 18, 39, 40
 tenuistriatus, 31
 truncatula, 31
 viator, 31
 limosa, *Limnæa*, 40, 41
 linearis, *Bunodera*, 34
 linearis, *Capillaria*, 263
 linearis, *Protostrongylus*, 175
 lineata, *Ascaridia*, 137
 lineatus, *Mesocestoides*, 78
 lingua, *Cryptocotyle*, 26
 litteratus, *Mesocestoides*, 78

- Loa, 218
 extraocularis, 219
 loa, 204, 218
 longemucronatus, Globocephalus, 167
 longibursatum, Trichonema, 153, 154
 longicaudum, Oesophagostomum, 158
 longicollis, Capillaria, 264
 longicornis, Bythinia, 20
 longipes, Capillaria, 263
 longistipes, Haemonchus, 193
 longulum, Dipylidium, 101
 Loossia, 25
 Lota maculosa, 71
 vulgaris, 71
 Loxotrema, 25
 lucida, Metroliaesthes, 102
 lucius, Esox, 43, 71
 lumbricoides, Ascaris, 129
 lunatus, Haemonchus, 193
 luteostoma, Ampullaria, 28, 31
 Lynx fasciatus, 25
 lyrata, Ostertagia, 186
- M
- Macracanthorhynchus, 272
 catulinus, 273
 hirudinaceus, 272
 macrostomum, Dicrocoelium, 16
 maculipennis, Anopheles, 207, 209
 maculosa, Ascaridia, 138
 maculosa, Helix, 93
 maculosa, Lota, 71
 madagascariensis, Raillietina, 92
 magalhãesii, Diofilaria, 207
 magna, Anophoccephala, 80
 magna, Fasciola, 32
 malayanum, Euparyphium, 41, 42
 malayi, Microfilaria [Filaria], 221
 mamillana, Anoplocephala, 80, 81
 mansoni, Diphylobothrium, 68, 72
 mansoni, Oxyspirura, 247, 248
 mansoni, Schistosoma, 48, 50
 mansoni, Sparganum, 72
 Mansonioides africanus, 210
 uniformis, 210
 marginata, Belascaris, 133
 marginatus, Planorbis, 15
 maritima, Ascaris, 132
 marshalli, Ostertagia, 187
 marshalli, Setaria, 217
 martis, Filaria, 205
 massino, Lepoderma, 12
 mastigodes, Oxyuris, 141
 mauretanicus, Tarentola, 102
 mauritanicus, Nematodirus, 196
 mazzantii, Harmostomum, 46
 Mecistocirrus, 196
 digitatus, 197, 198
 fordii, 198
 gibsoni, 198
 tagumai, 198
 medinensis, Dracunculus, 222
 megaloccephala, Ascaris, 131
 megalops, Hymenolepis (Weinlandia), 107
 megastoma, Habronema, 225
 Melania, 26, 28
 Melania hongkongensis, 20
 libertina, 20
 melanotus, Idus, 18
 meleagris, Hymenolepis, 106
 meleagris-gallopavo, Capillaria, 264
 Melolontha melolontha, 273
 mentulata, Ostertagia, 189
 mergorum, Eustrongylides, 241
 Mermithidae, 128
 meromyarian, 123
 Mesocestoides, 77
 lineatus, 78
 litteratus, 78
 perlatus, 78
 Mesocestoididae, 77
 Metagonimus, 25
 yokogawai, 25, 26
 Metastrongylidae, 171
 Metastrongylus, 171
 apri, 171, 172
 brevivaginus, 173
 elongatus, 172
 salmi, 172
 metidjensis, Planorbis corneus, 48
 Metorchis, 20
 albidus, 21
 orientalis, 21
 xanthosomus, 21
 Metroliaesthes, 102
 lucida, 102
 mettami, Trichonema (Cylicodontophorus), 155
 michiganensis, Alaria, 54
 microcotyle, Raillietina (Skrjabinia), 94
 Microfilaria, 220
 auquieri, 221
 diurna, 219
 guyanensis, 221
 lewisii, 221
 malayi, 221
 nuda, 221
 philippinensis, 221
 powelli, 221
 romanorum, 221
 sanguinis equi africana, 221
 seguini, 221
 streptocerca, 221
 tucumana, 221
 microstoma, Habronema, 224
 Microtetrameses inflatus, 241
 Microtremas, 22
 truncatum, 22
 minima, Anoplocephala, 81
 minor, Gastrodiscus, 61
 minor, Lagocephilascaris, 134
 minor, Triodontophorus, 151
 minuta, Ascocotyle, 26
 minuta, Felis, 16
 minutum, Trichonema, 154
 minutus, Echinorhynchus, 269
 miracidium, 8
 molitor, Tenebrio, 105, 106
 Moniezia, 82
 alba, 83
 benedeni, 83
 denticulata, 83
 expansa, 82
 pallida, 83

Moniliformis, 274
 moniliformis, 274
 monnigi, Gongylonema, 235, 236
 Monocercus, 77
 Monogenea, 5
 Monorchotrema, 26
 taichui, 26
 taihokui, 26
 Monostomidæ, 34
 Monostomum, 35
 montgomeryi, Trichonema (Cylicotoichus), 155
 mopsus, Gymnopleurus, 235
 mordens, Physaloptera, 243
 moschata, Cairina, 247
 mucronata, Blaps, 275
 mucronatum, Craterostomum, 151
 Muellerius, 175
 capillaris, 175, 176
 Mugil cephalus, 23, 24
 japonicus, 23
 Multiceps, 111
 gaigeri, 115
 glomeratus, 116
 multiceps, 115
 serialis, 115
 multiceps, Tænia (Multiceps), 115, 116
 multipapillosa, Parafilaria, 205
 murina, Tænia, 104
 Musca domestica, 98, 225
 muscæ, Habronema, 223, 224
 musculosa, Hymenolepis, 106, 108
 mutabile, Cycloccelum, 35
 mutabilis, Raillietina, 94
 mystax, Toxocara, 133
 Myzomyia superpicta, 207
 Myzorhynchus pseudopictus, 207

N

nagpurensis, Raillietina, 94
 nana, Hymenolepis, 103, 104, 105
 Nanophyetus salmicola, 25
 nasicola, Syngamus, 162
 nassatum, Trichonema (Cylicocyclus), 154
 nasuta, Acuaria (Dispharynx), 238
 natalensis, Limnæa, 31, 32, 48
 natans, Trapa, 34
 nebulosus, Onthophagus, 230
 Necator, 166
 americanus, 166
 suillus, 166
 Necatorinæ, 165
 Nematelminthes, 121
 Nematodes (Nematoda), 121
 Nematodirus, 193
 abnormalis, 194
 dromedarii, 196
 filicollis, 194
 furcatus, 196
 helvetianus, 196
 leporis, 196
 mauritanicus, 196
 spathiger, 194
 Neoascaris, 131
 nervosa, Cotugnia cuneata var., 96
 nitidellus, Segmentina, 33
 nobilis, Hypothalmichthys, 20

nocens, Heterophyes, 23
 nodulosum, Amidostomum, 199, 200
 nölleri, Diplopylidium, 101
 nosophora, Blanfordia, 26
 nosophora, Katayama, 26, 49
 Notocotylidæ, 36
 Notocotylus, 37
 ægyptiacus, 37
 attenuatus, 37
 noveboracensis, Parametorchis, 21
 novella, Tænia, 115
 noverca, Opisthorchis, 19
 nuda, Microfilaria, 221
 Numenius arquatus, 14
 Numida ptilorhyncha, 16
 Nycticorax, 26

O

oahuensis, Limnæa, 31
 obovale, Typhlococelum, 36
 obscurus, Tenebrio, 105
 obtusipes, Potamon, 28
 obvelata, Syphacia, 143
 occidentalis, Ostertagia, 188
 occidentalis, Physa, 39
 ochmanni, Filaria, 207
 Oenetrodrilus, 97
 ocreatus, Protostrongylus, 174, 175
 octocolata, Herpobdella, 107
 oculi, Agamofilaria, 220
 oerlevi, Dipylidium, 101
 Oesophagodontus robustus, 151
 Oesophagostominæ, 157
 Oesophagostomum, 157
 apiostomum, 158, 159
 asperum, 158
 brumpti, 158, 159
 columbianum, 157, 158, 159
 dentatum, 158
 longicaudum, 158
 radiatum, 158, 159
 stephanostomum, 158, 159
 venulosum, 158
 olivaceus, Planorbis, 48
 Ollulanus, 198
 tricuspis, 198
 Onchocerca, 211
 armillata, 214
 bovis, 214
 cæcutiens, 212
 cervicalis, 213
 fasciata, 214
 gibsoni, 213
 gutturosa, 214
 indica, 214
 lienalis, 214
 reticulata, 213
 volvulus, 212
 Oncicola, 273
 canis, 273
 onicola, 274
 Oncomelania hupensis, 49
 oncophora, Cooperia, 183
 Onchorhynchus, 25
 perryi, 71
 Oniticeilus fulvus, 235
 Onitis irroratus, 235

- Onthophagus bedeli*, 230, 235
 hecate, 229, 234
 nebulosus, 230
 pennsylvanicus, 234
 taurus, 235
ophthalmica, *Cypria*, 107, 109
Opisthorchidae, 18
Opisthorchis, 18
 caninus, 19
 felineus, 18, 19
 noverca, 19
 pseudofelineus, 19
 simulans, 19
 viverrini, 19
 wardi, 19
oregonensis, *Diaptomus*, 70
orientalis, *Metorchis*, 21
orientalis, *Trichostrongylus*, 181
orispinum, *Epomidiostomum*, 202
ornatum, *Trichonema* (*Cylicostomum*), 154
Ornithostrongylus, 189
 quadriradiatus, 189, 190
orthocœlium, *Paramphistomum*, 57
oscar, *Episthmium*, 44
Oslerus osleri, 177
ostertagi, *Ostertagia*, 185
Ostertagia, 184
 bullosa, 188
 circumcincta, 186
 lyrata, 186
 marshalli, 187
 mentulata, 189
 occidentalis, 188
 ostertagi, 185
 tricuspis, 188
 trifida, 188
 trifurcata, 187
 turkestanica, 188
ovatus, *Echinorhynchus*, 274
ovatus, *Prosthogonimus*, 13, 14
ovina, *Chabertia*, 159
ovis, *Ascaris*, 129
ovis, *Cysticercus*, 116
ovis, *Eurytrema*, 17, 18
ovis, *Skrjabinema*, 143
ovis, *Tænia*, 115, 116
ovis, *Trichuris*, 260, 261
ovum, *Cypripis*, 107
Oxyascaridae, 128
Oxyspirura, 247
 mansoni, 247, 248
 parvovum, 247
Oxyuridae, 128, 140
Oxyuris, 140
 compar, 141
 curvula, 141
 equi, 141
 incognita, 141
 mastigodes, 141
 poculum, 141
ozzardi, *Filaria*, 219, 221
- P
- pachicephalus*, *Hystrichis*, 255
pachyscelis, *Gaigeria*, 169
pacitæ, *Physaloptera*, 244
pallida, *Moniezia*, 83
Palonia frontalis, 60
paloniae, *Homalogaster*, 62
palpebralis, *Agamofilaria*, 220
palustris, *Limnæa*, 41
pancreaticum, *Eurytrema*, 17, 18
papillosa, *Heterakis*, 136
papillosus, *Strongyloides*, 145
Parabronema, 226
 skrjabini, 226
paradoxa, *Simondsia*, 229
Parafilaria, 205
 multipapillosa, 205
Parafossarulus striatulus, 20
Paragonimus, 27
 kellicotti, 28
 ringeri, 27
 westermanii, 27, 28
Paralipsa gularis, 106
Parametorchis, 21
 complexus, 21
 noveboracensis, 21
Paramonostomum, 38
 alveatum, 38
Paramphistomida, 55
Paramphistomidae, 55
Paramphistomoidea, 55
Paramphistomum, 56
 anisocotylea, 56
 cervi, 56
 explanatum, 57
 gotoi, 56
 ichikawai, 56
 ijimai, 57
 orthocœlium, 57
paranecator, *Acheilostoma*, 170
Paranoplocephala, 81
Parapelecus, 20
Parascaris, 131
Parastrigea, 53
 robusta, 53
Parathelphusa sinensis, 28
paraulum, *Echinostoma*, 40
Pardalis, 274
pardalis, *Echinopardalis*, 274
Paroniella, 91
Paropisthorchis, 19
Paruterininae, 97, 102
parva, *Pseudorasbora*, 21
parvuincinata, *Railletina*, 94
parvovum, *Oxyspirura*, 247
parvula, *Hymenolepis* (*Weinlandia*), 107
parvum, *Diphyllbothrium*, 71
parvum, *Eurytrema*, 17
pasqualei, *Joyeuxia*, 101
Passalurus ambiguus, 141
pateratum, *Trichonema* (*Cylicocercus*), 155
pectinata, *Cooperia*, 182, 183
pectinifera, *Streptocara*, 239
pellucidus, *Prosthogonimus*, 14
penetrans, *Railletina*, 94
penicillaris, *Culex*, 207
pennsylvanicus, *Onthophagus*, 234
peregra, *Limnæa*, 40
perfoliata, *Anoplocephala*, 80
perfoliatus, *Echinochasmus*, 43
pergracilis, *Trichostrongylus*, 181
Periplaneta americana, 275

- perlatus, *Mesosestoides*, 78
 Pernis apivorus, 19
 perryi, *Oncorhynchus*, 71
 persicus, *Heterophyes*, 24
 perspicillum, *Ascaridia*, 137
 perstans, *Acanthocheilonema*, 205, 208
 pervia, *Limnaea*, 31
 pfeifferi, *Planorbis*, 48, 50
 Phæneus splendidulus, 273
 Pharyngostomum, 54
 cordatum, 55
 Pheretima, 97
 philippina, *Tænia*, 114
 philippinensis, *Homalogaster*, 62
 philippinensis, *Microfilaria*, 221
 Philometridæ, 221
 Philophthalmidæ, 29
 Philophthalmus gralli, 29
 phlebotomum, *Bunostomum*, 169
 Phyllobothriinae, 63, 75
 Physa alexandrina, 48
 fontinalis, 31
 occidentalis, 39
 Physaloptera, 242
 caucasica, 242, 243
 gemina, 244
 mordens, 243
 pacitæ, 244
 præputialis, 243
 rara, 244
 truncata, 244, 245
 Physalopterinae, 241
 Physocephalus, 230
 cristatus, 230
 sexalatus, 230
 Physopsis africana, 32, 48, 49
 globosa, 48
 Piestocystis, 76, 78
 variabilis, 79
 Pinna, 251
 pintneri, *Hexastichorchis*, 86
 pipiens, *Culex*, 207, 210
 Pisidium fontinale, 15
 pisiformis, *Cysticercus*, 116
 pisiformis, *Tænia*, 115, 116
 Plagiorchis, 11
 Plagiorhynchus, 271
 formosus, 271
 Planorbis, 53
 antiquensis, 48
 boissyi, 48
 centimetralis, 48
 cœnosus, 33
 complanatus, 15
 corneus, 40, 48
 corneus, var. *metidjensis*, 48
 exustus, 50
 guadeloupensis, 48
 largillierti, 33
 marginatus, 15
 olivaceus, 48
 pfeifferi, 48, 50
 planorbis, 41
 rotundatus, 37
 schmackeri, 33
 Planorbis sudanicus, 48
 umbilicatus, 15
 Platodes, 3
 Platyhelminthes, 3
 Platynosomum, 16
 arietis, 16
 fastosum, 16
 Plecoglossus, 26
 plerocercoid, 76
 plica, *Capillaria*, 263
 plicata, *Anoplocephala*, 80
 poculatum, *Trichonema*, 154
 poculum, *Oxyuris*, 141
 poeli, *Elaeophora*, 215
 poirieri, *Homalogaster*, 62
 polonica, *Bilharziella*, 51
 Polycephalus, 111
 Polycercus, 77
 polymorpha, *Dreysensia*, 18
 Polymorphus, 269
 boschadis, 269
 polymyarian, 123
 Porcellio lævis, 238
 Porrocæcum, 134
 crassum, 134
 Potamobius astacus, 269
 Potamon dehaani, 28
 obtusipes, 28
 sinensis, 28
 potamophilia, *Eleotris*, 55
 potanini, *Lepoderma*, 12
 Poteriosomum, 156
 imparidentatum, 156
 rátzii, 156
 powelli, *Microfilaria*, 221
 præputialis, *Physaloptera*, 243
 prasinus, *Cyclops*, 70
 pretoriensis, *Hodotermes*, 227
 prionodes, *Trichonema* (*Cylicobrachytus*), 155
 probolurus, *Trichostrongylus*, 180, 181
 Probstmayria vivipara, 139
 proceroid, 70
 Procyon psora pacifica, 25
 proglottina, *Davainea*, 77, 90, 91
 Prognopylidium, 100
 Prohemistomum, 53
 appendiculatum, 53
 industrium, 54
 proliferum, *Sparganum* (*Gatesius*), 72, 73
 Prosostomata, 6
 Prosthogonimus, 13
 anatinus, 14
 brauni, 14
 cuneatus, 13, 14
 furcifer, 276
 intercalandus, 13
 japonicus, 14
 ovatus, 13, 14
 pellucidus, 14
 rudolphi, 14
 skrjabini, 14
 Protostrongylidæ, 171
 Protostrongylus, 171, 174
 linearis, 175
 ocreatus, 174, 175
 rufescens, 175, 178
 unciphorus, 175
 Prymnoprium, 13
 Pseudamphistomum, 21

Pseudamphistomum danubiense, 22
truncatum, 22
Pseudodiscus, 58
collinsii, 58
stanleyii, 58
watsoni, 58
pseudoechinobothrida, Raillietina, 94
pseudofelineus, *Opisthorchis*, 19
pseudopictus, *Myzorhynchus*, 207
Pseudorasbora, 20, 26
parva, 21
pseudoscutellaris, *Aedes*, 210
Pseudotelphusa iturbei, 28
Psilochasmus, 45
lecithosus, 45
Psilostomida, 44
psora, *Procyon*, 25
Pterygodermatites, 248
ptilorrhyncha, *Numida*, 16
pudendotectus, *Chærostrongylus*, 172, 173
pulchrum, *Gongylonema*, 233, 235
Pulex irritans, 99
pulex, *Daphnia*, 239, 241
pulex, *Gammarus*, 107, 241, 269
pulicis, *Filaria*, 240
pullæ, *Hymenolepis*, 106
punctata, *Cooperia*, 183
putaustralis, *Heterakis*, 136
Pycnocelus (Leucophæa) surinamensis, 248
Pyradus cingulatus, 26

Q

quadricornis, *Cyclops*, 223
quadrimaculata, *Libellula*, 13
quadriradiatus, *Ornithostrongylus*, 189, 190
quinquecoronatum, *Diplopylidium*, 101

R

radiatum, *Cesophagostomum*, 158, 159
radiatum, *Trichonema (Cylicocycclus)*, 154
radicola, *Heterodera*, 141
raillieti, *Diphylobothrium*, 68, 72
raillieti, *Sparganum*, 72
Raillietina, 91, 93
anatina, 94
asiatica, 92
birmanica, 94
cecticillus, 93
clerci, 94
cohnii, 94
crassula, 94
demerariensis, 92
echinobothrida, 92, 93, 94
formosana, 93
grobbeni, 94
madagascariensis, 92
mutabilis, 94
nagpurensis, 94
parviuncinata, 94
penetrans, 94
pseudoechinobothrida, 94
tetragona, 93, 94
volzii, 94
Raillietostrongylus, 167
samoensis, 167
Rana tigrina, 68

ranarum, *Diphylobothrium*, 68
ranarum, *Ligula*, 68
ransomi, *Gongylonema*, 233
Ransomia, 91
rara, *Physaloptera*, 244
rarus, *Schistogonimus*, 14
rathouisi, *Fasciolopsis*, 33
rátzii, *Poteriostomum*, 156
rebelle, *Eurytrema*, 276
reconditum, *Acanthocheilonema*, 209
recurvatum, *Echinoparyphium*, 41
redia, 8
Reditænia, 111
renalis, *Diectophyme*, 253
repens, *Dirofilaria*, 207
reptans, *Diphylobothrium*, 68
reptans, *Sparganum*, 68
reticulata, *Onchocerca*, 213
retusa, *Capillaria*, 264
revolutum, *Echinostoma*, 39
Rhabditidæ, 128, 143
Rhipicephalus sanguineus, 209
rhodesii, *Thelazia*, 245
Rhodeus sinensis, 55
Rictularia, 248
cahirensis, 249
ringeri, *Paragonimus*, 27
robusta, *Parastrigea*, 53
robustus, *Cheiracanthus*, 250
robustus, *Cesophagodontus*, 151
romanorum, *Microfilaria*, 221
rosseteri, *Echinocotyle*, 109
Rossicotrema, 24
donicum, 24
venustum, 24
rossicum, *Dipylidium*, 101
rossii, *Anopheles*, 210
rostrata, *Candona*, 107
rotundatus, *Planorbis*, 37
Roundworms, 121
rubella, *Limnæa*, 31
rubidus, *Hyostrongylus*, 183
rudolphii, *Prosthogonimus*, 14
rufescens, *Protostrongylus*, 175, 178
rufus, *Aphodius*, 229
rugatus, *Trichostrongylus*, 179
rustica, *Hymenolepis (Weinlandia)*, 106
rutilus, *Leuciscus*, 18, 21

S

sacer, *Scarabæus (Ateuchus)*, 230, 232, 235
saginata, *Tænia*, 111, 112, 113
sagitta, *Cordophilus*, 211
sagittatum, *Trichonema (Cylicostomum)*, 154
salmi, *Metastrongylus*, 172
salmincola, *Nanophyetus*, 25
Salmo, 25
samoensis, *Globocephalus [Raillietostrongylus]*, 167
sanguineus, *Rhipicephalus*, 209
sanguinis equi africana, *Microfilaria*, 221
sanguinis hominis diurna, *Filaria*, 204
sanguinis hominis nocturna, *Filaria*, 204
sanguinolenta, *Spirocerca*, 231
Sarcocheilichthys, 20
satyri, *Bertiella*, 81

- satyrus, *Xyloryctes*, 273
scarabæus sacer, 230, 232, 235
 variolosus, 230, 232
Scardinius erythrophthalmus, 24
Scaurus striatus, 106
Schistogonimus, 14
 rarus, 14
Schistosoma, 46
 bomfordi, 49, 50
 bovis, 49, 50
 cattoi, 49
 crassum, 49
 hæmatobium, 47, 48, 50
 incognitum, 51
 indicum, 50
 japonicum, 49, 50
 mansoni, 48, 50
 spindalis, 50
 spindalis, var. *africana*, 50
 turkestanicum, 50, 51
Schistosomatidæ, 46
schmackeri, *Planorbis*, 33
schreberi, *Caccobius*, 235
scutata, *Spiroptera*, 233
secundus, *Gastrodiscus*, 61
Segmentina largillierti, 33
 nitidellus, 33
seguini, *Microfilaria*, 221
serialis, *Tænia* (*Multiceps*), 115, 116
serrata, *Tænia*, 115
serrata, *Trichuris*, 260
serratus, *Triodontophorus*, 150, 151
Sesarma dehaani, 28
Setaria, 215
 bernardi, 218
 digitata, 217
 equina, 216
 labiato-papillosa, 216
 marshalli, 217
setigera, *Hymenolepis*, 107
sexalatus, *Physocephalus*, 230
sexcoronatum, *Dipylidium*, 101
siamensis, *Cheiracanthus*, 250
siamensis, *Fischoederius*, 60
silacea, *Chrysops*, 219
similis, *Astacus* (*Cambaroides*), 28
similis, *Hæmonchus*, 192
Simondsia paradoxa, 229
simulans, *Opisthorchis*, 19
Simulium damnosum, 212
sinensis, *Anopheles*, 210
sinensis, *Clonorchis*, 20
sinensis, *Eriocheir*, 28
sinensis, *Potamon* (*Parathelphusa*), 28
sinensis, *Rhodeus*, 55
sinicus, *Bos*, 49
sisowi, *Tracheophilus*, 36
sitiens, *Culex*, 210
Skrjabinema ovis, 143
skrjabini, *Epomidiostomum*, 201, 202
skrjabini, *Parabronema*, 226
skrjabini, *Prosthogonimus*, 14
skrjabini, *Trichuris*, 261
Skrjabinia, 91
 cesticillus, 94
 columbæ, 94
 microcotyle, 94
 solum, *Tænia*, 111, 112
Southwellia, 98
 gallarum, 98
Sparganum, 68
 baxteri, 72, 73
 mansoni, 72
 proliferum, 72, 73
 raillietii, 72
 reptans, 68
spathiger, *Nematodirus*, 194
spatiosus, *Carmyerius*, 61
sphenoides, *Amœbotænia*, 97
spindalis, *Schistosoma*, 50
spinifera, *Fasciolopsis*, 33
spinigerum, *Gnathostoma*, 250
spinosa, *Akis*, 106
spinosus, *Diaptomus*, 107
spiralis, *Acuaria* (*Dispharynx*), 238
spiralis, *Trichinella*, 256
Spirocerca, 231
 arctica, 232
 felineus, 233
 sanguinolenta, 231
Spiroptera, 237
 cinnamata, 213
 scutata, 233
spirovoluta, *Fillaria*, 220
Spirurata, 202
Spiruridæ, 223
Spirurinae, 223
Spirozoidea, 202
splendidulus, *Phanæus*, 273
sporocyst, 8
stagnalis, *Limnæa*, 18, 39, 40
Stannosoma, 26
 armatum, 26
 formosanum, 26
stanleyi, *Pseudodiscus*, 58
Stegomyia calopus, 221
 fasciata, 207
stenocephala, *Uncinaria*, 165, 170
Stephanopharynx, 59
 compactus, 59
stephanostomum, *Esophagostomum*, 158, 159
Stephanurinae, 160
Stephanurus dentatus, 160
stercoralis, *Strongyloides*, 144, 145
Stilesia, 83, 87
 globipunctata, 88
 hepatica, 87
 vittata, 88
Stizostedion canadense-griseum, 71
 vitreum, 71
Stomoxys calcitrans, 108, 225
strenuus, *Cyclops*, 70
streptocara, 239
 pectinifera, 239
streptocerca, *Microfilaria* [*Agamofilaria*], 221
striatulus, *Parafossarulus*, 20
striatus, *Scaurus*, 106
Strigea, 52
 gracilis, 52
 tarda, 53
Strigeidæ, 52
Strobilocercus, 111
Strongylidæ, 147

- strongylina, Arduenna, 228
 Strongylinae, 148
 Strongyloidea, 146
 Strongyloides, 144
 canis, 146
 papillosus, 145
 stercoralis, 144, 145
 suis, 146
 vituli, 146
 westeri, 145
 Strongylus, 149
 anseris, 200
 asini, 148, 149
 canis bronchialis, 177
 edentatus, 148, 149, 150
 equinus, 148, 149
 vulgaris, 148, 149
 strumosum, Corynosoma, 271
 strumosum, Trichosoma, 264
 studeri, Bertiella, 81
 sturmi, Gymnopleurus, 230, 232, 235
 styphlocerca, Ascaridia, 138
 subæqualis, Cylicospirura, 233
 subtilis, Gongylonema, 233
 Subulura, 138
 brumpti, 139
 differens, 139
 suctoria, 139
 Subulurinae, 138
 suctoria, Subulura, 139
 sudanea, Avitellina, 86
 sudanicus, Planorbis, 48
 sufrartyfex, Euparyphium, 42
 suilla, Ascaris, 129
 suillus, Necator, 166
 suinum, Euparyphium, 42
 suis, Ascaris, 129
 suis, Strongyloides, 146
 suis, Trichocephalus, 258
 superpicta, Myzomyia, 207
 surinamensis, Pycnocelus (Leucophæa), 248
 Sus cristatus, 44, 229
 sylvaticus, Geotrupes, 98
 Syngaminae, 161
 Syngamus, 161
 dispar, 163
 kingi, 163
 laryngeus, 162
 nasicola, 162
 trachea, 161
 trachealis, 161
 Synthetocaulus, 171, 174
 Syphacia obvelata, 143
- T
- Tænia, 111
 africana, 114
 antarctica, 115
 balaniceps, 115
 brachysoma, 115
 brauni, 115, 116
 bremneri, 114
 cænurus, 115
 confusa, 114
 crassicolis, 115
 flavopunctata, 105
 gaigeri, 115, 116
 Tænia hominis, 114
 hydatigena, 114, 115, 116
 infantis, 114
 krabbei, 115, 116
 multiceps, 115, 116
 murina, 104
 novella, 115
 ovis, 115, 116
 philippina, 114
 pisiformis, 115, 116
 saginata, 111, 112, 113
 serialis, 115, 116
 serrata, 115
 solium, 111, 112
 tæniaformis, 111, 114, 115, 116
 tonkinensis, 114
 varesina, 105
 tæniaformis, Tænia, 111, 114, 115, 116
 Tæniarhynchus, 111
 Tæniidae, 110
 Tæniidea, 63, 75
 Tæniinea, 63, 75
 Tænioinei, 63
 Tæniorhynchus fuscipennatus, 209
 tagumai, Mecistocirrus, 198
 taichui, Monorchotrema, 26
 taihokui, Monorchotrema, 26
 taniguchii, Filaria, 219
 Tapeworms, 62
 tarandi, Cysticercus, 116
 tarda, Strigea, 53
 Tarentola mauretanica, 102
 Tatus, 274
 taurus, Onthophagus, 235
 Tenebrio molitor, 105, 106
 obscurus, 105
 tenuicauda, Craterostomum, 151
 tenuicollis, Cysticercus, 116
 tenuicollis, Tridontophorus, 151
 tenuistrois, Hymenolepis, 107
 tenuis, Acanthophorus, 240
 tenuis, Cotignia cuneata, var., 96
 tenuis, Trichostrongylus, 181
 tenuistriata, Limnæa, 31
 Ternidens, 159
 deminutus, 159
 Testifrons cristata, 44
 tetraacanthum, Trichonema (Cylicostomum), 154
 Tetracotyle typica, 53
 tetragona, Raillietina, 93, 94
 Tetragoneuria, 13
 Tetrameres, 240
 travassosi, 241
 Tetraphyllidea, 75
 Tetrarhynchidea, 63
 texana, Ascaris, 132
 Thelazia, 245
 alfortensis, 246
 callipæda, 246
 gulosa, 246
 lacrymalis, 246
 leesei, 247
 rhodesii, 245
 Thelaziinae, 245
 thomasi, CEsophagostomum stephanostomum, var., 158, 159

- Threadworms, 121
 Thymallus, 71
 Thysanosoma, 88
 actinioides, 89
 Thysanosominae, 88
 Tiara, 28
 tichodroma, Hymenolepis, 106
 tigrina, Rana, 68
 Tinca, 54
 tinca, 18
 Tinea granella, 106
 togoi, Aedes, 210
 tonkinensis, Tania, 114
 torquata, Houttuynia, 96
 Toxascaris, 133
 leonina, 133
 limbata, 133
 Toxocara, 133
 canis, 133
 mystax, 133
 trachea, Syngamus, 161
 trachealis, Syngamus, 161
 Tracheophilus, 36
 sisowi, 36
 Tragulus, 62
 Trapa bicornis, 34
 natans, 34
 travassosi, Tetrameres, 241
 Trematoda (Trematodes), 5
 Tribolium ferrugineum, 106
 Trichina, 255
 Trichinella, 255
 spiralis, 256
 Trichinellidae, 255
 Trichinellinae, 255
 Trichinelloidea, 255
 trichiura, Trichuris, 258
 Trichocephalos, 258
 Trichocephalus, 258
 affinis, 261
 apri, 258
 crenatus, 258
 depressiusculus, 260
 dispar, 258
 echinophyllus, 261
 hominis, 258
 suis, 258
 Trichodectes canis, 99
 Trichonema, 152, 154
 adersi, 154
 aegyptiacum, 154
 alveatum, 155
 asymetricum, 155
 auriculatum, 152, 154
 barbatum, 154
 bicornatum, 155
 bidentatum, 155
 breviscapulatum, 155
 calicatum, 154
 catinatum, 155
 coronatum, 154
 elongatum, 154
 euproctus, 155
 goldi, 155
 hybridum, 154
 ihlei, 155
 insigne, 154
 labiatum, 154
 labratum, 154
 leptostomum, 154
 longibursatum, 153, 154
 mettami, 155
 minutum, 154
 montgomeryi, 155
 nassatum, 154
 ornatum, 154
 pateratum, 155
 poculatum, 154
 prionodes, 155
 radiatum, 154
 sagittatum, 154
 tetracanthum, 154
 triramosum, 154
 ultrajectinum, 155
 Trichoneminae, 152
 Trichosoma, 261
 strumosum, 264
 Trichosomoides crassicauda, 255
 Trichosomoidinae, 255
 Trichostrongylidae, 178
 Trichostrongylinae, 178
 Trichostrongylus, 179, 182
 axei, 181
 capricola, 180
 colubriformis, 180
 extenuatus, 178, 179
 falculatus, 180
 instabilis, 180
 orientalis, 181
 pergracilis, 181
 probolurus, 180, 181
 rugatus, 179
 tenuis, 181
 vitrinus, 178, 179, 180
 Trichurinæ, 258
 Trichuris, 258
 cameli, 261
 campanula, 260
 discolor, 261
 globulosa, 261
 ovis, 260, 261
 serrata, 260
 skrjabini, 261
 trichiura, 258
 vulpis, 259, 260
 tricolor, Hystrichis, 255
 tricornata, Verodunia, 58
 tricuspis, Ollulanus, 198
 tricuspis, Ostertagia, 188
 trifida, Ostertagia, 188
 trifurcata, Ostertagia, 187
 trigonocephalum, Bunostomum, 168
 trinchessii, Diplopylidium, 100, 101, 102
 Triodontophorus, 150
 brevicauda, 151
 intermedius, 151
 minor, 151
 serratus, 150, 151
 tenuicollis, 151
 triramosum, Trichonema (Cylicocycclus), 154
 Troglotreumatidae, 27
 tropica, Isidora, 31, 48
 Tropidocerca, 240
 fissispina, 240

Tropidonotus, 68
Tropisurus, 240
 americanus, 241
 confusus, 241
 fissispinus, 240
 gallineis, 241
 gigas, 241
 inflatus, 241
 truncata, *Physaloptera*, 244, 245
 truncatula, *Limnæa*, 31
 truncatum, *Microtrema*, 22
 truncatum, *Pseudamphistomum*, 22
 tuberosa, *Eliocharis*, 34
 tucumana, *Microfilaria*, 221
 tumidus, *Hyptiasmus*, 35
 turkestanica, *Ostertagia*, 188
 turkestanicum, *Schistosoma*, 50, 51
 Typhlocœlum, 35
 obovale, 36
 typica, *Tetracotyle*, 53

U

ultrajectinum, *Trichonema* (*Cylicodontophorus*), 155
umbilicatus, *Planorbis*, 15
Uncinaria, 169
 stenocephala, 165, 170
uncinata, *Acuaria* (*Echinuria*), 239
uncinatum, *Epomidiostomum*, 202
unciphorus, *Protostrongylus*, 175
uniformis, *Mansonioides*, 210
urosululatus, *Globocephalus*, 167

V

varesina, *Tænia*, 105
variabilis, *Piestocystis*, 79
variegatus, *Aedes*, 210
variegatus, *Limax*, 91
variolosus, *Scarabæus*, 230, 232
vasorum, *Angiostrongylus*, 177
venulosum, *Esophagostomum*, 158
venustum, *Rossicotrema*, 24
vermicularis, *Enterobius*, 142
Verodunia tricornata, 58
verrucosa, *Catatropis*, 38
verrucosum, *Gongylonema*, 234, 235
vesicularis, *Heterakis*, 136
vexans, *Culex*, 207
viator, *Limnæa*, 31
vigintivasus, *Davainoides*, 95
villosa, *Hymenolepis*, 106

viridis, *Cyclops*, 107
vitreum, *Stizostedion*, 71
vitrinus, *Trichostrongylus*, 178, 179, 180
vittata, *Stilesia*, 88
vittatus, *Aphodius*, 234
vituli, *Strongyloides*, 146
vitulorum, *Ascaris*, 131
viverrini, *Opisthorchis*, 19
Vivipara, 53
vivipara, *Probstmayria*, 139
viviparus, *Dietyocaulus*, 174
volvulus, *Onchocerca*, 212
volzii, *Raillietina*, 94
vryburgi, *Agriostomum*, 165
vulgaris, *Diaptomus*, 110
vulgaris, *Lota*, 71
vulgaris, *Strongylus* (*Delafondia*), 148, 149, 150
Vulpes lagopus, 232
vulpis, *Trichuris*, 259, 260

W

walkeri, *Dipylidium*, 101
wardi, *Opisthorchis*, 19
Wardium, 103
watsoni, *Pseudodiscus*, 58
Watsonius, 58
Weinlandia, 103
 carioca, 106
 collaris, 107
 coronula, 107
 gracilis, 107
 megalops, 107
 parvula, 107
 rustica, 106
westeri, *Strongyloides*, 145
westermanii, *Paragonimus*, 27, 28
Wuchereria, 209
 bancrofti, 204, 210

X

xanthosomus, *Metorchis*, 21
Xenopsylla cheopis, 106
Xyloryctes satyrus, 273

Y

Yokogawa, 25
yokogawai, *Bilharziella*, 51
yokogawai, *Metagonimus*, 25, 26

Z

Zacco, 26

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